FIELDIANA

Botany

NEW SERIES, NO. 39

A Revision of the South American Species of *Brunfelsia* (Solanaceae)

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London SW7 5BD
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Accepted July 2, 1996
Published August 31, 1998
Publication 1496

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

ISSN 0015-0746
PRINTED IN THE UNITED STATES OF AMERICA

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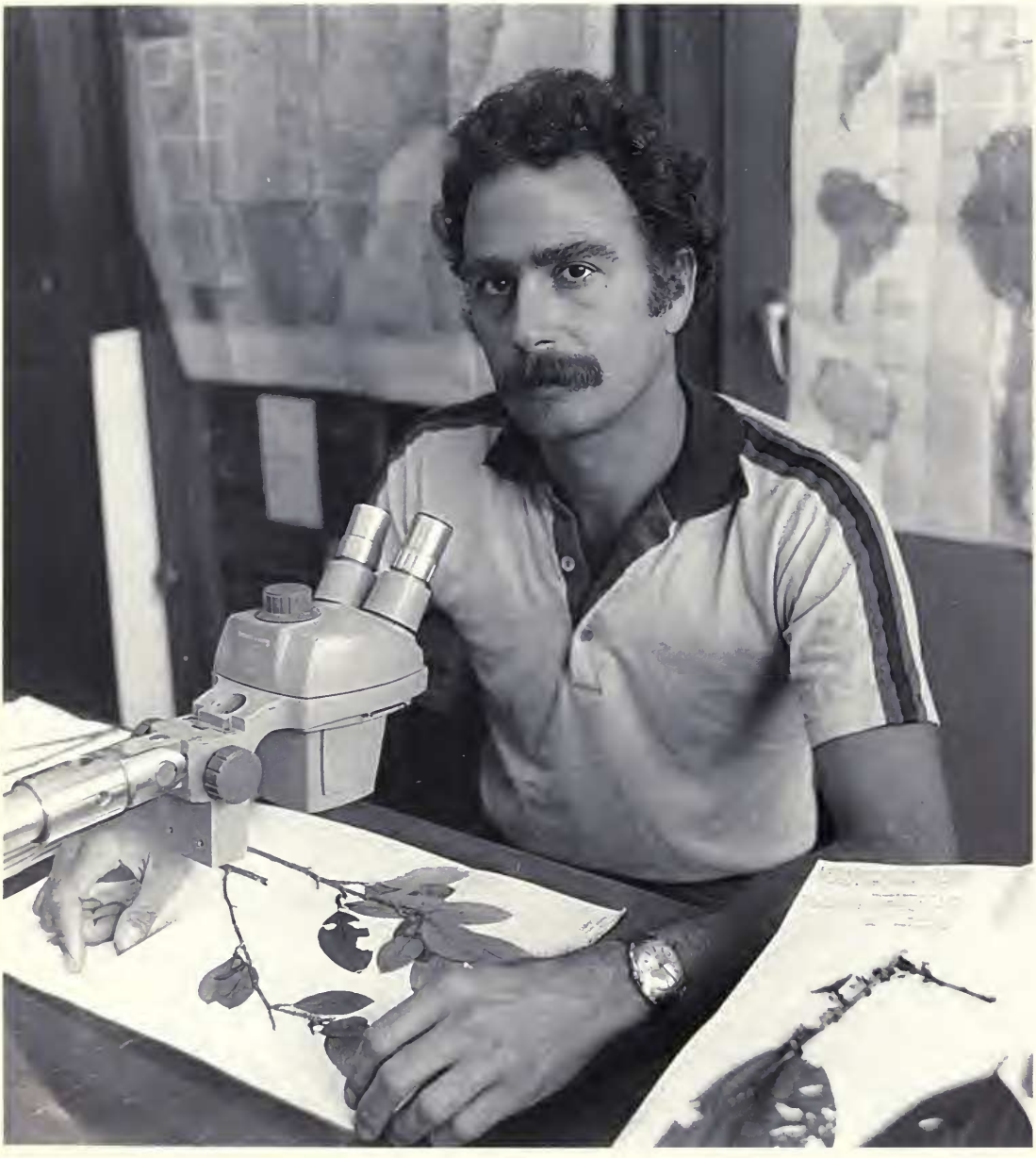

Tim Plowman

Foreword

The idea for this monograph emerged from somewhat unusual circumstances. On March 29, 1942, ethnobotanist and plant explorer Richard Evans Schultes arrived at the Kofán Indian village of Conejo, on the banks of the Río Sucumbíos in the remote rain forests of southern Colombia. In the midst of his first sojourn in the Amazon, with the goal of surveying medicinal plants and arrow poisons, Schultes found himself immersed in a world of phytochemical wizardry unlike anything he had ever known. Psychoactive and toxic plants touched every aspect of the lives of the Kofán. The most important and sacred of their plants was the hallucinogen *Banisteriopsis caapi*, or yagé, the "vine of the soul." When Schultes inquired how often the people imbibed yagé, his informant's response suggested that the question had no meaning. During illness, of course, and in the wake of a death. In times of need or hardship. At certain passages in life. When a young body of six has his initial haircut, or when he kills for the first time. And naturally, the shaman suggested, a youth will drink yagé at puberty, when his nose and ears are pierced and he obtains the right to wear the tail feathers of the macaw. As a young man, he may drink it at his leisure to improve his hunting technique or simply to flaunt his physical prowess. The message that Schultes received was that the Kofán took yagé whenever they felt like it. At least once a week, and no doubt on any occasion that warranted it, such as the eve of his own departure from Conejo a fortnight later. With the people dancing, the men facing the women in long lines moving forward and then back, turning from side to side, the dancers stamping the ground lightly in time with the drums, this solitary student of plants, a man who in time would inspire a generation of ethnobotanists, took yagé with, as he would recall 50 years later, "the whole damn village."

The next morning, his face still painted and his mind swirling with the sounds of chants, Schultes paddled up the Sucumbíos in a dugout canoe. His head throbbed. Unbeknownst to him, the preparation had contained bark of *tsontinb"k'o*, the cold fever tree, together with *su-tim-ba-che*, a root said by the Kofán to cause a "drunk worse than yagé." Indeed, it had. Despite his discomfort, Schultes made a note to investigate the admixtures at length. Thirty years later he did, by dispatching his protégé, Timothy Plowman, to the Putumayo. After 15 months in the field in South and Central America and the Caribbean, Tim Plowman emerged with a definitive study, a monographic revision of the genus *Brunfelsia*, including descriptions of several new species and varieties. The plant that Schultes drank at Conejo and that gave him such a headache is now known as *Brunfelsia grandiflora* subsp. *schultesii*.

Tim Plowman approached botanical research with the intensity and rigor of a scientist, the courage of his mentor, and the flair of a poet. His first Colombian excursion set the pattern of his career. Arriving in Bogotá, he traveled south to the valley of Sibundoy, where he contacted Pedro Juajibioy, a Kamsa Indian healer who as a boy guided Schultes into the upper Putumayo. Tim and Pedro retraced that journey to reach a Kofán settlement on the Río Guamués, also visited by Schultes in 1942. The Kofán recognized *B. grandiflora* as *tsontinba"k"á*. Another of Schultes's students, Homer Pinkley, who spent a year among the tribe in 1965, had written that their shaman occasionally ingested the plant in order to diagnose disease. This observation supported other reports dating back to the 19th century that suggested the plant might be hallucinogenic. Plowman wanted to know. At Santa Rosa on the Río Guamués he found *B. grandiflora* commonly cultivated in house yards, but he also met an old shaman who brought him from the forest a rare but related plant named for the tapir because of its inordinate strength as a drug. Plowman immediately recognized the plant as a new species, which he later named *Brunfelsia chiricaspi* after the Quechua word meaning cold tree. He asked the old man to prepare it, but the shaman refused. He described the plant as a dangerous messenger of the forest and disavowed any knowledge of taking it for visions. Tim persisted. Eventually the shaman agreed, although reluctantly and only on the condition that Pedro also drink the preparation.

The drug, an extract from the bark, was murky brown and bitter to swallow. Tim felt the effects within ten minutes: a tingling sensation such as one feels when the blood rushes back to a limb that has fallen asleep. Only in this case the sensation grew to a maddening intensity, spreading from his lips and fingertips toward the center of his body, progressing up his spine to the base of his skull in waves of cold that flooded over his consciousness. His breathing collapsed. Dizzy

with vertigo, he lost all muscular control and fell to the mud floor of the shaman's hut. In horror he realized that he was frothing at the mouth. An hour passed. Paralyzed and tormented by an excruciating pain in his stomach, he remained only vaguely aware of where he was—on the earth, face to face with three snarling dogs fighting over the vomit that had spread in a pool around his head.

The shaman, noticing his plight, did what shamans normally do under such circumstances: He went to bed. Desperate to escape the sensation, half-blinded by the drug, and incapable of walking, Tim and Pedro stumbled and crawled through the forest for two hours until finally, toward dawn, they reached the village of San Antonio, where they were staying in an abandoned jail. As light came to the forest, they crawled into their hammocks, where they remained, motionless, for two days. Pedro Juajibioy, whose experience as a folk healer had taken him on a thousand flights of the spirit, summed up the experience succinctly: "The world was spinning around me like a great blue wheel. I felt that I was going to die."

This story reveals something of the character of this remarkable young scholar, a man of adventure, grace, generosity, kindness, modesty, and honor, whose academic achievements in time might well have surpassed even those of his famous mentor, Richard Evans Schultes, the "Father of Ethnobotany." Sadly, Tim's life was cut short by cruel circumstances. His untimely death at the age of 45 from AIDS on January 7, 1989, severed a career of immense promise. Already far on the way as one of the most discerning, original, and effective naturalists of the century, Tim was a gentleman, a friend of everyone, an understanding and devoted teacher, an intellectual of extraordinary depth, and a tireless and demanding researcher happy to share his experience and counsel with whomever sought his advice.

Tim Plowman's interest in and love of plants developed when he was a child growing up in the temperate woodlands surrounding Harrisburg, Pennsylvania. An avid collector even as a boy, his passion for plants grew into the central metaphor of his life. After attending college at Cornell University, he went as a graduate student to the Botanical Museum of Harvard University. Such was his promise that even before enrolling in graduate school, Tim was dispatched by Schultes to the Amazon on an expedition that would define the course of his professional life. In the fall of 1966 Tim returned from Brazil flush with excitement and fully committed to spending the rest of his life in pursuit of the mysteries of the tropical rain forest.

His dissertation, with its thorough bibliographic research, precise and deliberate taxonomic and ethnobotanical insights, elegant prose, and exquisite line drawings, set the standard of excellence by which he would operate throughout his professional career. By the time his Ph.D. was officially conferred, in 1974, Tim was already deeply involved in the project for which he will always be remembered, a 15-year effort to decipher the complex taxonomy of *Erythroxylum* and to study the ethnobotany of coca, the sacred leaf of the Andes and the notorious source of cocaine. Of Tim's 80 published scientific papers, 46 are related to his work on *Erythroxylum*, and his position as the world's authority on the genus enabled him to speak eloquently and powerfully in defense of the traditional use of coca by beleaguered indigenous peoples of the Andes and northwest Amazon.

In 1978 Tim left Harvard for the Field Museum of Natural History, where he became tenured in 1983 and was appointed curator in 1988. If Tim grew up at the Botanical Museum at Harvard, he came into his own at the Field Museum, and his years there were both the happiest and most productive of his remarkable career. His interdisciplinary interests in systematics, ethnobotany, and ethnopharmacology led him to interact with an increasingly diverse group of scholars that included not only fellow botanists but also archaeologists, phytochemists, ethnographers, and pharmacologists. In addition to carrying out an active scientific research program as co-principal investigator of the National Science Foundations "Projeto Flora Amazonica," he served on the editorial boards of numerous journals, including *Flora Neotropical Monographs*, *Advances in Economic Botany*, *Journal of Psychoactive Drugs*, and *Journal of Ethnopharmacology*. Between 1984 and 1988 he was co-editor-in-chief of the *Journal of Ethnopharmacology* and the scientific editor of *Fieldiana*. He was vice president of the Beneficial Plant Research Association, a fellow of the Linnean Society, and a member of many professional societies, including the American Society of Plant Taxonomists, the Society of Economic Botany, the Council of Biology Editors, the Society of Ethnobiology, and the New England Botanical Club. As chairman of the botany department of the Field Museum of Natural History (1986–1988), Tim secured a substantial increase in Na-

tional Science Foundation funding for the herbarium and developed a new facility for the curation of economic collections. His enthusiasm, spirit of cooperation, professional rigor, and passionate commitment to botany proved infectious, and under his leadership, morale within the botany department soared.

Credentials alone, however, present but a shadow of the man who affected so many lives in such profound ways. For Tim, life was but a vehicle for seeking understanding and for expressing freedom. If there is a word to describe Timothy Plowman it would be freedom, and he lived with the conviction that every person had the right to pursue his or her own path unshackled by the burdens of social convention. Equally at ease in the tranquil world of plants and the society of people, Tim was charismatic, and those privileged to have spent time with him often developed a respect that bordered on reverence, for he was a true renaissance scholar, a man out of time, whose breadth of interests and passions went far beyond the boundaries of his beloved field of botany.

But it is as a botanist and intrepid plant explorer that Tim will be best remembered. He spent more than five years of his life in the most remote and inhospitable regions of the Andes and Amazon, making more than 15,000 collections of unsurpassed quality. He always considered his time in the field a privilege, and he never failed to remember his fellow botanists toiling away in the less romantic confines of the herbaria. Tim seemed to have a Rolodex in his head that recorded the name of every specialist in every group of plants, and he was constantly on the lookout for specimens that might prove useful to a distant colleague. He collected everything. His voucher specimens were not only complete but aesthetically beautiful, and whenever possible he augmented them with invaluable collections of live material. Living plants, many new to science and collected first by Tim, may be found in botanical gardens throughout the world.

In the rain forests of the Amazon Tim felt the fullness of life. He marveled at the thousand themes, the infinitude of form, shape, and texture that so clearly mocked the terminology of temperate botany. He always traveled in the forest as a student, and his commitment to ethnobotany grew in part from his direct experience with the indigenous peoples who understood the plants in ways that he believed he could only hope to emulate. To be in the forest, he said, was to be in Eden, and to say the names of the plants was to recite the names of the gods. He believed that all forms of life were manifestations of the sacred. Hence, for Tim, biological and cultural diversity represented far more than the foundation of stability; they were articles of faith, fundamental truths that indicated the way things were supposed to be.

Tim had a special affinity for Indians, and his uncanny ability to gain their trust and confidence was one measure of the deep respect he had for their way of life. He empathized with their world view, which defined man as but one element inextricably linked to the whole of creation. It was this unique cosmological perspective, he believed, that enabled the Indians to comprehend implicitly the intricate ecological balance of the forest he loved so dearly. Tim viewed with pain, dismay, and increasing anger the other world view, in which man stands apart, that now threatens the forest with devastation. It was one of his fondest hopes that the lessons of ethnobotany might ultimately facilitate a dialogue between these two world views such that folk wisdom might temper and guide the inevitable development processes that today ride roughshod over much of Earth. The many of us who loved him as a brother and respected him as a colleague can do no better service to his memory than continue our own struggles to make his dream a reality.

—Wade Davis

Editors' Preface

Tim Plowman not only was a "botanist's botanist," he also inspired a whole generation of young taxonomists with his enthusiasm for plants in both the field and herbarium.

The study of the systematics of the South American species of *Brunfelsia* was the subject of his Ph.D. research while he was at Harvard University. After receiving his Ph.D. in 1974, Tim worked mainly on *Erythroxylum*, but *Brunfelsia* remained an area of special interest for him. He was preparing a major revision of the group, using his dissertation as a basis and backing up with further study and extensive field work, when he died in 1989.

In 1994 Tim's colleagues at the Field Museum of Natural History in Chicago sent the manuscript, together with various notes and archival material, to one of us (S.K.) to assess whether the work could be brought to completion. We are very pleased to have been able to do this, both because it will make available this extensive study of an interesting group of Solanaceae and because it will serve as a tribute to the work of a well-liked and respected colleague.

In taking the working manuscript and bringing it to publication, we tried throughout to keep in mind Tim Plowman's concept of the group and changed his work as little as possible. Most of the manuscript remains essentially unaltered, but where necessary we rearranged some sections and augmented others in line with Tim's own publications, notes, and records. The only major departure from this approach is where we felt a need to update the manuscript in the light of works published since Dr. Plowman's death. Such updates usually take the form of explanatory notes in the text that are clearly indicated as being editors' contributions.

To this end, the key was revised to incorporate additional species published (by Plowman) since the original manuscript was written. The order of specimen citations is Plowman's. In some places reasoning is not clear, but we chose not to change the order. Specimens not cited in the original work but seen by Dr. Plowman and recorded in his notes and in the herbarium at the Field Museum were added; they are marked with an asterisk and are inserted in order of collector at the end of each state or province. These later records are included in the distribution maps. Infraspecific taxa are not indicated on the maps because Plowman's later annotations were only to specific rank and could not be integrated with distributions of infraspecific taxa. Additional references, some of them Plowman's own subsequent publications, were inserted; like the additional specimens, these are marked in the bibliography with an asterisk.

Several new combinations remained unpublished at the time of Tim's death and are validated here. The authority for these combinations should be simply Plowman, as they represent Tim's assessment of the status and rank of the taxa and should be attributed solely to him.

The additional bibliography in Appendix II lists references to publications that postdate the original manuscript and that we believe will provide a better understanding of the current state of knowledge in the genus.

This revision of *Brunfelsia* is the product of Tim Plowman's research, but we accept sole responsibility for any errors of interpretation or presentation.

—S. Knapp
J. R. Press

Franciscea hydrangeæformis.

Opposite: Brunfelsia hydrangeiformis subsp. *hydrangeiformis* (originally as *Franciscea hydrangeiformis*), illustration of type. Illustration reproduced from J. E. Pohl, *Plantarum Brasiliae Icones et Descriptiones* (1826).

A Revision of the South American Species of *Brunfelsia* (Solanaceae)

Timothy C. Plowman†
S. Knapp and J. R. Press, Editors

I. Materials and Methods

Beginning in the fall of 1968, I began studying the genus *Brunfelsia* L. in the field, both in South America and in the West Indies. During trips varying in duration from a few weeks to several months, I studied many of the species of *Brunfelsia* in their natural habitats, giving special attention to population variability and ecological conditions. At this time I collected extensive material for morphological, cytological, and chemical studies, including numerous herbarium specimens and living material in the form of seeds and cuttings for propagation in the greenhouse. I also took this opportunity to investigate the medicinal properties and uses of the plants among native people who still possess an intimate knowledge of plant medicines. I learned about these aspects of the plants not only by inquiring among native healers but also by taking the medicines myself (Plowman, 1977).

Many of the species I had hoped to see in the field could not be found in localities where they were formerly collected, due to both the sporadic occurrence of the plants and the destruction of their habitats by man. At other times, the plants were found but without much sought-after flowers or fruits.

To acquire a historical perspective of the genus, to properly typify specific names, and to view as much morphological variation as possible, I borrowed herbarium specimens from many institutions in Europe, South America, and the United States. These specimens, numbering about 3,000 [the number at the time of his thesis in 1974, although many more subsequently were examined by Plowman—*Eds.*], provided the basis for the study. This material was organized according to the recommendations outlined by Leenhouts's (1968) *A Guide to the Practice of Herbarium Taxonomy*, which offered many helpful suggestions.

Some 55 morphological characters were observed and measured or scored on a character flow sheet. For many specimens it was not possible to record all the characters, especially those of the fruits, which are rarely, if ever, collected, and those of the corolla, which is usually poorly pressed and often glued fast to the herbarium sheet, precluding dissection of the stamen and pistil. The characters and their variation were analyzed according to methods outlined and discussed in Benson (1962), Davis and Heywood (1963), Lawrence (1965), and Anderson (1967), among others. Descriptions of the various taxa were prepared using characters observed in herbarium specimens and in living plants. In many cases the color of the flowers and other evanescent characters were not known with certainty; as a result, the completeness of the description varies somewhat from species to species.

Pollen was acetolyzed according to the procedure of Erdtman (1960). Unacetolyzed pollen grains were also examined with the aid of a scanning electron microscope. Cytological material was collected in the field and in the greenhouse and fixed in Carnoy's solution (absolute alcohol: glacial acetic acid, 3:1), then stored in 95% alcohol. Chromosomes were stained with acetocarmine.

Bulk material for chemical analysis was collected in the field and dried in the open sun or in special drying ovens. This material was sent to Mr. Jan-Erik Lindgren at the Department of Toxicology, Karolinska Institutet, Stockholm, Sweden, and to Dr. John Leary, Massachusetts College of Pharmacy, Boston, Massachusetts. Extracts of these plants were tested for alkaloids and general constituents using precipitation reactions and gas and thin-layer chromatography [see Plowman, 1977; Lloyd et al., 1985; Schultes & Raffauf, 1990, 1991—*Eds.*]. In addition, simple tests for alkaloids were performed by Prof. Robert F. Raffauf and myself on fresh plants growing in the greenhouse. Extracts were prepared from fresh

material of five species and tested for alkaloids by precipitation reactions.

Sixteen species were grown in the greenhouses of the Biological Laboratories, Cambridge, Massachusetts; the Arnold Arboretum, Jamaica Plain; and the Botanical Research Station of Northeastern University in Woburn, Massachusetts. [Other specimens were cultivated at the Field Museum of Natural History, Chicago, Illinois, in later years.—*Eds.*] Material was propagated from both seeds and cuttings collected in the wild or from cultivated plants. Crosses were attempted between as many species as possible. The living plants were also a valuable source of those morphological characters that are lost in dried specimens and permitted observations to be made on the growth and development of various organs, particularly the inflorescence.

A considerable amount of time in this study was devoted to searching the botanical, chemical, and pharmacological literature for references to *Brunfelsia*. Only those works that are cited in the text are included in the bibliography.

All of the specimens cited in this work were examined by me unless they are denoted by "*non vidi*." The use of brackets in the citation of a collection number indicates that some uncertainty exists or, in the case of type materials, that the number appearing on the sheet was not given in the original citation of the specimen.

Finally, the use of taxonomic characters deserves some explanation. Of the 24 species of *Brunfelsia* that are recognized in South America, four are considered to possess one variety each in addition to the typical variety. The category of subspecies is here used for geographical or ecological races that show morphological differentiation from the typical form of the species. It should be noted, however, that the degree of differentiation and isolation varies from one species to another, so that the subspecific concepts are not entirely equivalent. Furthermore, variants exhibiting considerable differentiation exist within several subspecies (e.g., *B. grandiflora* subsp. *schultesii* Plowman, *B. brasiliensis* (Spreng.) L.B. Sm. & Downs subsp. *brasiliensis*). Subsequent workers in the genus may choose formally to recognize these as variants at infraspecific rank.

II. Taxonomic History of the Genus

The genus *Brunfelsia* was first described by Charles Plumier in 1703 in his *Catalogus Plantarum Americanarum*, commemorating the German herbalist Otto Brunfels (1464–1534). Brunfels was a Carthusian monk and physician who, in 1530, published an herbal, *Herbarum Vivae Eicones*, that, as the name indicates, included illustrations of living plants. This early work is outstanding for the high quality, accuracy, and naturalistic aspect of the woodcuts, which for the first time departed from the often copied and stylized illustrations of earlier herbals (Arber, 1912). Unfortunately, Plumier misspelled the genus name as "*Brunsfelsia*," an error that has tenaciously persisted in the literature [see D'Arcy, 1989—*Eds.*].

Simultaneously with his short description and diagnosis, Plumier published a rather good illustration of the flower and fruit of the plant, which is now known as *B. americana* L. The illustration was taken from a larger, more complete drawing that, along with more detailed descriptions in manuscript form, is kept at the Museum National d'Histoire Naturelle in Paris, France. The complete plate was published with a more complete description in 1756 in Burman's edition of Plumier's *Catalogus Plantarum Americanarum* (Fig. 1).

In the second edition of *Genera Plantarum* (1742), Linnaeus included *Brunfelsia*, based on Plumier's description. He classified *Brunfelsia* among the Pentandria Monogynia, indicating that the plant had five stamens (an aberrant condition that occasionally occurs in *B. americana*). It would thus seem that Linnaeus had access to specimens since Plumier failed to mention this character and it is not indicated in his drawing. Although there is no known specimen of *B. americana* in extant Linnaean herbaria, he did indicate with a symbol in the fifth edition of *Genera Plantarum* (1754) that he knew the genus from herbarium material.

In a letter to David Van Royen in 1767, Linnaeus mentioned that he did, in fact, see a specimen of the *Brunfelsia* of Plumier: "*Brunsfelsiam* Plumieri vidi exsiccatam, at illa forte a Tua specie diversa erat, ideoque nihil certi de ea potui pron-

→

FIG. 1. *Brunfelsia americana*. From Burmann's edition of Plumier's *Catalogus Plantae Americanarum* (1703).


TAB. LXV.
A
B
C
B
BRUNSFELSIA.
original drawing Plate II 83

unciare, nec Adansonii compilationes mihi suffecere" (Bonnet, 1895). Van Royen had sent Linnaeus a specimen (no. 257.1, LINN) that Linnaeus recognized as being different from Plumier's species. This plant is now referable to *B. undulata* Swartz.

The valid publication of the genus dates from 1753, when Linnaeus published *B. americana* in *Species Plantarum*, in which he followed the original misspelling of the genus. This was apparently an orthographical oversight on his part with which he was inconsistent in later works. For example, in the following year (1754), he used the correct spelling in *Genera Plantarum* but misspelled it in subsequent editions of *Species Plantarum*. In the *International Code of Botanical Nomenclature* (Greuter et al., 1994, p. 297), *Brunfelsia* is listed in Appendix IIIA as a conserved spelling [see also D'Arcy, 1989—*Eds.*].

The next important date in the history of the genus was 1826, when Pohl published seven new species from Brazil as the genus *Franciscea*, which he placed in the order Scrophularinae, close to *Browallia*. Each of Pohl's seven new species was accompanied by an excellent illustration (frontispiece, Figs. 22, 28, 31, 39, this work). Additional species were soon added to *Franciscea* by Chamisso and Schlechtendal (1827) and Hooker (1828).

However, as early as 1829, David Don published his observations on this group, in which he maintained that *Franciscea* did not differ significantly from *Brunfelsia*. He united the two genera under the earlier name *Brunfelsia* but published only one new combination, *B. uniflora* (Pohl) D. Don. Don also expressed the opinion, precocious for the time, that *Brunfelsia* belonged in the Solaneae (Solanaceae) rather than the Scrophularinae, an idea suggested even earlier by Antoine de Jussieu (1791).

Most authors of the time ignored Don's conclusions and continued to recognize *Brunfelsia* and *Franciscea* as distinct genera, primarily on the basis of the nature of the capsule and the length of the corolla tube (Bentham, 1835; G. Don, 1837; Endlicher, 1839; Meisner, 1840).

In 1846, however, in his monograph on the Scrophulariaceae for de Candolle's *Prodromus*, Bentham united *Franciscea* with *Brunfelsia*, observing that although the francisceas were distinguished by some authors, especially by the dry capsule, he himself had looked in vain for definitive structures; *B. latifolia* (Pohl) Benth. and *B. guianensis* Benth. had small flowers like the rest of the francisceas but capsules no less fleshy than those of *B. americana*, and in several species the fruit was completely unknown.

Bentham's treatment of *Brunfelsia* included 19 species, eight of which were formerly considered *Franciscea*. He divided the genus into three groups without rank: *Multiflorae* and *Uniflorae* (*Franciscea*) and *Longiflorae* (*Brunfelsia*), placed among the Salpiglossideae. This work bears the distinction of being the only revision of *Brunfelsia* that has attempted to encompass the entire genus. Bentham considered the Salpiglossideae to be a "suborder" (subfamily) of the Scrophulariaceae and noted their close affinity with the capsular Solanaceae, with which, he added, they might be better associated.

Shortly after Bentham's revision appeared, John Miers began publishing a series of papers on the Solanaceae consisting of taxonomic treatments, descriptions of new genera and species, and a major reorganization of the tribes into two families, the Solanaceae and the Atropaceae. These replaced the older concept of Solanaceae and included the Salpiglossideae of Bentham. The text of Miers's work was originally published in *The Annals and Magazine of Natural History* between 1849 and 1857 and later appeared bound together in two volumes accompanied by 87 plates under the name *Illustrations of South American Plants* (Miers, 1855, 1857). This extensive work remains a major source of information for solanaceous plants.

Miers (1849) erected the new family Atropaceae as a distinct group with imbricate or plicate corolla estivation that was intermediate between the Solanaceae (with valvate estivation) and the Scrophulariaceae (with imbricate estivation). The group included ten tribes, the last of which he named the Brunfelsiae. Miers firmly believed that *Brunfelsia* and *Franciscea* should be maintained as distinct genera, citing some ten differences that he considered diagnostic. Among these were the habit of the plants, the relative length and shape of the corolla, the color of the corolla, the shape of the anthers, the size and structure of the fruit, and the number of seeds per fruit.

Several points of difference indicated by Miers between *Brunfelsia* and *Franciscea* no longer stand when one considers the wide range of variation and many additional species that are now recognized. For example, he stated (1849, 1850) that brunfelsias are trees attaining 20 ft in height whereas francisceas are small shrubs. In fact, both low shrubs and small trees occur in about equal

numbers in both groups. Miers considered the fruit of *Brunfelsia* a fleshy drupe containing an indehiscent putamen and that of *Franciscea* a dehiscent capsule that splits along four vertical sutures. It is now clear that within both *Brunfelsia* and *Franciscea*, dehiscent and indehiscent, thin- and thick-walled, and fleshy and dry fruits occur. On the basis of limited material, Miers failed to recognize the overall similarities between these groups. However, several differences that he pointed out remain valid and serve to distinguish *Brunfelsia* and *Franciscea* as distinct sections of the genus.

Perhaps the most disturbing fact in Miers's study of *Brunfelsia* is his omission of *B. guianensis*, a species that Bentham (1846) described and commented on in the *Prodromus*. In Miers's otherwise complete list of new combinations, in which he transferred most of Bentham's new brunfelsias to *Franciscea*, *B. guianensis* is conspicuously missing. Since *B. guianensis* possesses several features that are intermediate between *Brunfelsia* and *Franciscea*, it seems that Miers perhaps simply ignored it because it blurred the sharp distinction he wanted to demonstrate.

The view of Bentham, to unite *Franciscea* with *Brunfelsia*, eventually prevailed over Miers's ideas, perhaps because of the wide distribution and general acceptance of de Candolle's *Prodromus*. Although some of Miers's conclusions have not gained acceptance in light of more recent knowledge, his extensive observations are nonetheless valuable to any taxonomist interested in the Solanaceae. For example, Bentham and Hooker (1873) drew heavily from Miers's data in describing the Solanaceae for *Genera Plantarum*.

There has been only one other major study of *Brunfelsia* since the time of Miers and Bentham. This is found in J.A. Schmidt's treatment of the Scrophulariaceae in Martius's *Flora Brasiliensis* in 1864. Although only Brazilian species were included, then numbering about ten, Schmidt made many sound taxonomic judgments and correctly reduced many names to synonyms. Until the present time, this work remained the standard reference for *Brunfelsia* in Brazil, which possesses the largest number of species of any country in South America. However, Schmidt's treatment is now out of date, as may be expected, and not without error.

In an attempt to clarify certain nomenclatural problems regarding his new species *Brunfelsia mire* Monach., Monachino (1953) offered a brief discussion of the names of the South American species. This was a work of limited value and provided little help in solving the taxonomic difficulties in the genus, being based primarily on the erroneous conclusions of others.

Besides the original descriptions of the plants, which for certain species are the only information available, only floristic works have provided accounts of the species in particular areas. Foremost among these, which are by no means of uniform quality, are the following works: *Flora of the British West Indian Islands* (Grisebach, 1861); *Botany of Porto Rico and the Virgin Islands* (Britton & Wilson, 1925); *Flora de Cuba* (Liogier, 1957); *Flora of Peru* (Macbride, 1962); *Flora Ilustrada Catarinense, Solanáceas* (Smith & Downs, 1966); *Flowering Plants of Jamaica* (Adams, 1972); and *Flora of Panama* (D'Arcy, 1974).

Table 1 summarizes the history of classification of *Brunfelsia*, including generic, tribal, and family placement. It should be noted under the heading "Family" that the groupings of the earlier botanists were not equivalent to our modern families of plants. These are included for historical purposes only.

III. Generic Relationships

Brunfelsia is a distinct genus that is not readily confused with other genera. It belongs to the tribe Salpiglossideae of the Solanaceae, as circumscribed by Bentham (1835, 1846, under Scrophulariaceae), Bentham and Hooker (1873), Wettstein (1895), and Baehni (1946). This group is considered the most advanced tribe of the Solanaceae[1] and resembles Scrophulariaceae in several characters, such as the zygomorphic corolla with somewhat imbricate estivation, the number of stamens reduced to four or two, and the capsular fruits. It is distinguished from the latter by intraxylary phloem (Metcalfe & Chalk, 1950) and from other Solanaceae by the estivation of the corolla and the number of stamens.

The closest relatives of *Brunfelsia* are *Browallia* L., a weedy herbaceous genus of two or pos-

[1] Although traditionally placed in the tribe Salpiglossideae and considered closely related to *Browallia* and *Salpiglossis*, results of recent phylogenetic studies using chloroplast DNA (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press) indicate that *Brunfelsia* may be better placed in a monophyletic group with the genera *Petunia*, *Fabiana*, and *Nierembergia*. The morphological evidence remains to be assessed.—*Eds.*

TABLE 1. Summary of historical classification of *Brunfelsia*.

Author	"Family"	Tribe	Genus
Linnaeus (1753)	Pentandria Monogynia		*Brunfelsia*
Swartz (1788)	Didynamia Angiospermae		*Brunfelsia*
Jussieu (1791)	Personatae		*Brunfelsia*
Pohl (1826)	Scrophularineae		*Franciscea* (excluding *Brunfelsia*)
D. Don (1829)	Solaneae		*Brunfelsia* (including *Franciscea*)
Bentham (1835)	Scrophularineae	Salpiglossideae	*Brunfelsia* *Franciscea*
G. Don (1837)	Solanaceae	Francisceae	*Brunfelsia* *Franciscea*
Endlicher (1839)	Scrophularineae	Salpiglossideae	*Brunfelsia* *Franciscea*
Bentham (1846)	Scrophulariaceae	Salpiglossideae	*Brunfelsia* (including *Franciscea*)
Miers (1849)	Atropaceae	Brunfelsiae	*Brunfelsia* *Franciscea*
Bentham and Hooker (1873)	Solanaceae	Salpiglossideae	*Brunfelsia* (including *Franciscea*)
Baillon (1888)	Scrophulariaceae	Salpiglossideae	*Brunfelsia* (including *Franciscea*)
Wettstein (1895)	Solanaceae	Salpiglossideae	*Brunfelsia* (including *Franciscea*)
Baehni (1946)	Solanaceae	Salpiglossideae	*Brunfelsia* (including *Franciscea*)
Hutchinson (1969)	Salpiglossidaceae		*Brunfelsia* (including *Franciscea*)
Plowman (1973)	Solanaceae	Salpiglossideae	*Brunfelsia* (including *Franciscea*)

sibly three heteromorphic species, and *Streptosolen* Miers, a monotypic Andean shrub genus. [*Plowmania* Hunz., a monotypic genus from montane Guatemala, first described as a species of *Brunfelsia*, is also considered to be closely related to *Brunfelsia* (see Hunziker & Subils, 1986).—*Eds.*] *Browallia* is distinguished from *Brunfelsia* by its herbaceous habit; by the filaments, which are greatly dilated and ciliate at the apex; by the broad, lamellate stigma, which has recurved margins, and by the dry capsule, which is dehiscent by four sutures. *Streptosolen* differs from *Brunfelsia* in having the corolla tube twisted at the base, the limb bright red-orange, and the filaments thickened at the apex. This shrub grows at high altitudes in the Andes from Colombia to Peru and is pollinated by hummingbirds.

The other genera of the Salpiglossideae are primarily annuals found in southern South America: *Salpiglossis* Ruiz and Pavón, *Schizanthus* Ruiz and Pavón, *Leptoglossis* Benth., *Reyesia* Clos, *Petunia* Juss., and *Schwenkia* L. (which also occurs in Africa). In addition, three genera of Australian shrubs are also placed in the tribe: *Duboisia* R. Br., with indehiscent, baccate fruits, and *Anthocercis* Labill. and *Anthotroche* Endl., with dehiscent, capsular fruits.[2]

[2] Since the time of the dissertation, these genera have been segregated as the endemic tribe Anthocercideae (Haegi, 1981), and additional genera have been described.—*Eds.*

Hutchinson (1969) elevated the Salpiglossideae to the rank of family (Salpiglossidaceae) with the explanation that the genera of this group consistently arrived next to Scrophulariaceae in his key to the families of plants of the world. This decision does not seem justified in view of the extensive evidence from morphology, anatomy, and chemistry, which links the Salpiglossideae with the Solanaceae.

The origin and relationships of the Salpiglossideae remain obscure. Baehni (1946) derived the group from two sources, the Solaneae via the subtribe Goetzeineae and the Atropeae via *Parabouchetia* Baillon. In the past, relationships at the generic and tribal levels in the Solanaceae were studied using relatively few characters, such as the curvature of the embryo, corolla estivation, number of anthers, or type of fruit. A definitive and in-depth evaluation of these higher relationships is needed in which many characters are considered simultaneously, including those from morphology, chemistry, anatomy, cytology, and other areas [see footnote 1—*Eds.*]

IV. General Morphology

Habit

All known species of *Brunfelsia* are woody shrubs, a few of which will become small trees.

No herbaceous members are known. In section *Brunfelsia*, certain species may reach 10–12 m in height (*B. jamaicensis* (Benth.) Griseb., *B. americana*, *B. lactea* Krug & Urb.). These are somewhat atypical, however, and most are only 2–3 m. Species of sections *Franciscea* and *Guianenses* are mostly medium-sized shrubs 1–3 m tall that form a component of the understory of the forest. *Brunfelsia grandiflora* D. Don of the western Amazon may become a small tree 4–5 m tall or, in the Brazilian state of Acre, may become lianoid in habit, attaining up to 10 m. *Brunfelsia latifolia* is the most diminutive species, often flowering when only 30 cm tall and rarely reaching 1 m in height.

Root

The roots of *Brunfelsia* are diffuse in the seedlings and young plants. However, mature plants often develop a deep, woody taproot. This is especially true in species of section *Brunfelsia*, which often grow in rocky areas. In section *Franciscea*, the central root may be more or less branched (Fig. 2).

Branching

Species of *Brunfelsia* may have one central trunk (*B. densifolia* Krug & Urb., *B. mire*, *B. chiricaspi* Plowman) or they may be branched to a greater or lesser extent from near the base, at times producing two or more main trunks (*B. australis* Benth., *B. grandiflora*, *B. brasiliensis*). In some cultivated species, root suckers often appear around the main trunk and form extensive clonal plants (*B. nitida* Benth., *B. undulata* Sw., *B. australis*).

In section *Brunfelsia*, the branches are often few and subvirgate, with few leaves at the end of a long, spindly branch (*B. undulata*, *B. splendida* Urb.). In sections *Franciscea* and *Guianenses*, the branches are more often diffuse or spreading and tend to arch over with age.

The branching pattern in *Brunfelsia* is sympodial. When the terminal bud ceases to grow, the shoot is perpetuated from one or more subterminal axillary buds or, rarely from the bracts of the inflorescence. In the new shoot, several prophylls are produced, followed by a gradual transition to mature leaves.

Leaf

The leaves of *Brunfelsia* are alternately arranged with 5/13 phyllotaxy. They may be scattered along the branchlets or crowded toward the apex, rarely subverticillate through periodic shortening of the internodes (*B. mire*, *B. hydrangeiformis* (Pohl) Benth., *B. rupestris* Plowman). The petiole is very short in relation to the leaf blade, varying from 1 to 10 mm in length. It is semiterete in section and canaliculate, and frequently becomes transversely cracked or corrugate with age or drying.

The leaves are simple with an entire margin. There is much variation in their size and shape, which provide important characters for distinguishing the species. In form, the blade may be elliptic to lanceolate; obovate to oblanceolate; or, rarely, spathulate, ovate, linear, or linear-lanceolate. Certain species are noted for great variability of leaf shape, sometimes in the same individual (*B. uniflora* (Pohl) D. Don, *B. americana*, *B. lactea*). In other species (*B. portoricensis* Krug & Urb., *B. densifolia*), the leaves of seedlings and young plants differ radically from the foliage of adult plants. At the apex, the leaves may be blunt, acute, or acuminate. It is of ecological interest that the leaves of species of wet, tropical forests are often acuminate in the form of a modified "drip tip" (*B. grandiflora*, *B. macrocarpa* Plowman, *B. chocoensis* Plowman, *B. amazonica* Morton).

In size, leaves may be 1–30 cm long and 0.1–15 cm wide. Leaf size may vary considerably within a species (e.g., *B. grandiflora*, 6–23 cm long) and is strongly influenced by local environmental conditions such as available light and moisture.

The leaf texture is mostly firm-membranaceous to subcoriaceous, often soft and rubbery to the touch. A few species (*B. splendida* Urb., *B. dwyeri* D'Arcy, *B. obovata* var. *coriacea* J. A. Schmidt, *B. rupestris*) are noted for their shiny, thick-coriaceous leaves. Coriaceous leaves also occur in certain populations of *B. uniflora* and *B. brasiliensis* that grow in unusually dry or exposed situations.

In color, the leaves are light to dark green and paler green beneath. Dark purple pigmentation due to anthocyanins is present in the young flush growth of several species (*B. pilosa* Plowman, *B. plicata* Urb., *B. undulata*). The leaves of *B. splendida* are particularly striking, being very dark green, almost black, and very shiny.

The nervation in *Brunfelsia* consists of the mid-

rib, which is completely submerged on the adaxial surface and prominent beneath, and three to 12 pairs of pinnate, lateral nerves. Each nerve spreads out from the costa and arcuately anastomoses with the next near the margin. The veinlets are finely reticulate and may be obscure or somewhat prominulous. The number of lateral nerves may be used to separate certain species (e.g., *B. martiana* Plowman from *B. guianensis*), but the angle of divergence and degree of arching are often variable. *Brunfelsia hydrangeiformis* is unique in having the midrib, nerves, and major veinlets sunken into a shallow depression or sulcus on the adaxial surface, creating a very uneven surface texture.

Indument

Most *Brunfelsia* species are essentially glabrous throughout, although the young leaves and flower buds may be sparsely puberulent in their earlier stages, becoming glabrous with age. In the pubescent species, trichomes are usually encountered in the twigs, leaves, pedicel, calyx, and corolla tube. In section *Franciscea*, the indument is best developed in *B. boliviana* Plowman, *B. brasiliensis*, *B. cuneifolia* J.A. Schmidt, *B. hydrangeiformis*, and *B. pilosa*, and to a much lesser extent in certain populations of *B. uniflora*, *B. pauciflora* (Cham. & Schltdl.) Benth., and *B. obovata* Benth. In section *Brunfelsia*, the following species may be pubescent: *B. americana*, *B. sinuata* A. Rich., *B. membranacea* Urb., and *B. jamaicensis*. Species of section *Guianenses* are entirely glabrous but occasionally have sparse glandular hairs on the petioles and pedicels (*B. burchellii* Plowman, *B. clandestina* Plowman) and ciliate or villous bract margins (*B. chocoensis*, *B. martiana*).

Uniseriate trichomes are found in both section *Brunfelsia* and section *Franciscea*. They may be either glandular or nonglandular, containing from two to ten cells. Glandular trichomes often have a single terminal, globose cell or may have one to several biseriate, terminal cells (*B. uniflora*). Several types of trichomes may occur together in the same organ, or only one type may be found. In Venezuelan populations of *B. uniflora*, the calyx and pedicel may bear short glandular trichomes, while the twigs and leaves may be pilose to villous with nonglandular hairs and a sharp demarcation at the attachment of the pedicel.

In section *Brunfelsia* (*B. americana*, *B. sinuata*), simple, branched trichomes also occur on the leaves. These have not been observed in section *Franciscea*.

The presence, location, and degree of pubescence appear to be highly variable in some species (*B. uniflora*, *B. pauciflora*, *B. americana*). Attempts have been made in the past to distinguish varieties solely (or essentially so) on the basis of the presence or absence of trichomes (*B. uniflora* var. *pubescens* (Benth.) R. E. D. Baker & N. W. Simmonds, *B. americana* var. *pubescens* Griseb., *B. pauciflora* var. *calycina* (Benth.) J. A. Schmidt, *B. brasiliensis* var. *acuminata* (Pohl) L. B. Sm. & Downs). Numerous intergradations in degree of pubescence are found in these species, and lacking correlation with other, more stable characters, it would be unwise to recognize these as "varieties." Indeed, variation can be observed within duplicates of a single collection. [This is also commonly the case in other Solanaceae (see Knapp, 1989).—*Eds.*] The greater development of pubescence is sometimes associated with plants growing in drier or more exposed habitats, suggesting that they may be environmentally induced forms or ecotypes. In any case, the unstable nature of these variants precludes their receiving formal taxonomic status. In other species, however, the type and location of trichomes, correlated with additional characters, can be useful in delimiting subspecies (*B. brasiliensis*, *B. hydrangeiformis*).

In relatively few species is the indument of diagnostic value at the specific level. *Brunfelsia pilosa* is characterized by long, pilose trichomes on the twigs, leaves, and calyces. *Brunfelsia brasiliensis* has a distinctive yellow-brown pubescence that is generally distributed in the plant. *Brunfelsia cuneifolia* usually has a villous calyx, a lower leaf surface, and twigs, although the type collection is nearly glabrous. *Brunfelsia boliviana* has villous-ciliate leaf margins and villous twigs.

Inflorescence

The inflorescence may be strictly terminal, axillary, or a combination of terminal and axillary in the same plant.

←

FIG. 2. Root of *Brunfelsia grandiflora* subsp. *schultesii*.

The inflorescence in *Brunfelsia* is basically a cincinnus or some reduction or variation thereof (Danert, 1958). In *Diccionario de Botánica*, Font Quer (1965) provided a succinct definition of the cincinnus as a uniparous cymose inflorescence in which the medial plane of each branchlet is placed transversely with respect to the medial plane of the subtending bract of the main axis (pseudaxis) and with the lateral branchlets alternately disposed to the right and left. It is a scorpioid cyme in which the various pseudaxes (branchlets) do not all fall in the same plane.

The cincinnal cyme is a primitive type of inflorescence in the Solanaceae in that the lateral branchlets are essentially undifferentiated from the primary inflorescence axis. In view of the otherwise advanced position of *Brunfelsia* in the family, this is a striking feature [but see Olmstead & Palmer, 1992—*Eds.*].

In *Brunfelsia* species with well-developed inflorescences, the cincinnus is elaborated as follows: a single flower terminates the main or lateral axis and is subtended by one to three (rarely more) small, caducous bracts, each of which bears a bud in its axil. From one or more of these bracts arise lateral branchlets, which are usually highly reduced, each of which bears a terminal flower and usually two tiny bracts, one on each side. Each successive branchlet is formed at right angles to its subtending bract. In secondary and higher orders of branching, only one of the two bracts forms a branchlet, alternating to the right and left. This gives the older branches of the inflorescence a zigzag pattern, produced by the remaining pedicel scars (e.g., *B. latifolia*, *B. grandiflora*).

The most common form of inflorescence in the genus is few-flowered, compact, and sessile, with the branchlets of the cincinnus very reduced. In some species, the individual branchlets are often difficult to distinguish, so condensed are the flower clusters. Two species (*B. grandiflora*, *B. brasiliensis*) are known to develop open, lax inflorescences in which the branches may be elongated to greater or lesser extent. In other species (*B. mire*, *B. hydrangeiformis*), many flowers are produced but without elongation of the inflorescence branchlets, resulting in a very dense, capituliform cyme. In still others, the inflorescence consists of a single flower (*B. americana*, *B. dwyeri*, *B. macrocarpa*, *B. uniflora*) or one to three flowers (*B. pilosa*, *B. australis*, *B. cuneifolia*, *B. rupestris*).

Great plasticity is found in the expression of the inflorescence in a single species and is due to both environmental and genetic factors. Species that frequently produce many flowers (*B. grandiflora*, *B. hydrangeiformis*) in a well-developed inflorescence may have only a few flowers per cluster. Other species that usually are single-flowered (*B. pilosa*, *B. amazonica*) will occasionally develop two or three flowers. Under normal forest conditions, *B. chiricaspi* bears up to seven flowers in the inflorescence; however, one collection (*Kennedy 1386*), growing in full sun in a cut-over place, had more than 20 flowers. Similar light-related responses have been observed in *B. grandiflora* (*Plowman 2535*). This variability, evident to some extent in most of the species, limits the usefulness of the number of flowers per inflorescence as a taxonomic character, particularly in the construction of keys.

Flower

The flowers of *Brunfelsia* species are composed of the following parts: a pedicel; a five-lobed calyx; a long-tubular corolla with a five-lobed limb; two pairs of stamens inserted in the upper part of the corolla tube; and a pistil, the style of which nearly equals the tube. There are major differences among the flowers of the three sections of the genus; however, within a section, the flowers are remarkably similar with only a few minor exceptions. Differences that do occur and that are important in distinguishing the species are found in the relative sizes of the flowers and their parts.

The flowers are slightly zygomorphic with bilateral symmetry. This is observable in the calyx, which occasionally has unequal lobes; in the curvature of the corolla tube; in the unequal limb; and in the didynamous stamens. The stamens and style are curved toward the "back" or posterior side of the flower, in line with the uppermost corolla lobe, and the anthers and stigma are brought very close to that side of the tube. This construction is probably advantageous in pollination because the proboscis of the pollinating insect (Lepidoptera) is most likely to descend along this part of the tube (see Fig. 3).

The flowers of section *Brunfelsia* are very large with a long tube and a usually showy white limb that fades to yellow (Figs. 4, 5). They are extremely fragrant in the evening and apparently are pollinated by night-flying moths (Sphingidae). In section *Franciscea* the flowers are smaller and

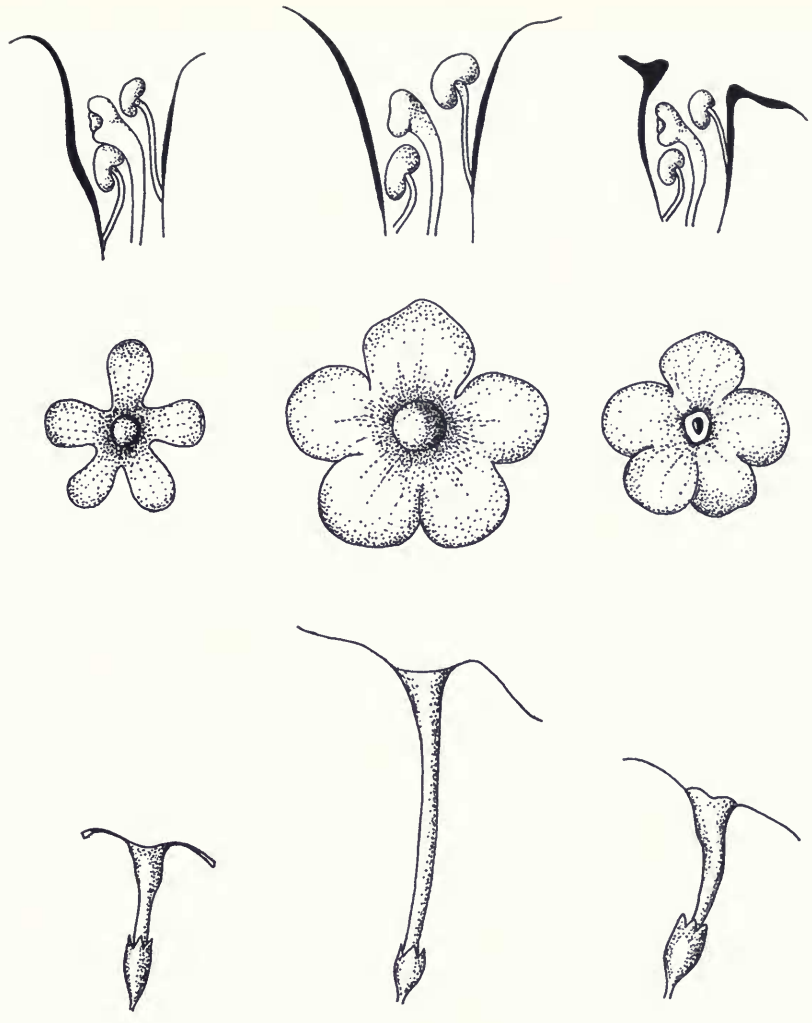

FIG. 3. Floral structure of the sections of *Brunfelsia*.

have a shorter tube with a purple limb and a white eye at the center. They are usually not fragrant and are pollinated by day-flying butterflies from several different families. Species of section *Guianenses* have small whitish or greenish flowers with a short tube and a relatively narrow limb. They are said to be fragrant, but the pollinators are unknown.

Calyx

The calyx is actinomorphic or slightly zygomorphic, in form tubular to campanulate and often somewhat inflated. It varies in length from 3 to 35 mm. In section *Brunfelsia* the calyx is very short compared to the corolla tube; in sections *Franciscea* and *Guianenses* it is usually about half as long,

although in some species (*B. pauciflora*, *B. hydrangeiformis*) it may equal the corolla tube.

The calyx teeth or lobes are triangular, ovate or lanceolate, and valvate in bud. In section *Brunfelsia* they are often blunt with a few ciliate trichomes. In sections *Franciscea* and *Guianenses* the teeth are acute or acuminate, and the ciliate margins are much reduced or obsolete.

The calyx is glabrous or may be furnished with glandular (*B. boliviana*, *B. pauciflora*, *B. uniflora*) or nonglandular (*B. pilosa*, *B. brasiliensis*) trichomes. In color it is usually some light shade of green to yellowish (*B. undulata*, *B. grandiflora*) or purplish (*B. pilosa*, *B. jamaicensis*).

The size and shape of the calyx, as well as its pubescence, are taxonomically important in specific delimitation. In most species the calyx is terete, but in a few (*B. obovata*, *B. boliviana*, *B. cuneifolia*, *B. nitida*) it is five-angled at the sinuses and concave at the lobes.

The nature of the calyx in fruit also provides useful characters. The calyx is usually persistent in fruit but scarcely accrescent. It may become thicker and firmer in texture and in section *Franciscea* frequently bears lenticular outgrowths near the base. It may split along one or more sides to accommodate the developing fruit, persisting only at the base, or it may increase in girth to partially or completely enclose the fruit at maturity (*B. hydrangeiformis*, *B. pauciflora*, *B. brasiliensis*). *Brunfelsia macrocarpa* is unique in the genus in having a large, truly accrescent calyx that becomes thick and leathery, completely enclosing the fruit.

Corolla

The corolla differs significantly in the three sections of *Brunfelsia*, as mentioned above (Fig. 3). In section *Brunfelsia* the corolla tube is very long, from 6 to 24 times as long as the calyx. It becomes gradually dilated near the apex but never curved or constricted at the mouth (Fig. 5). The limb usually is held at an angle to the tube. The five lobes may be narrow or broad, plane or undulate to crenate at the margin. In color the corolla tube is greenish or white; the limb is usually pure white when it first opens, turning yellow with age. *Brunfelsia americana* and *B. lactea* may be streaked with purple. Anomalous species are *B. cestroides* A. Rich. and *B. purpurea* Griseb. of Cuba, the flowers of which are said to be purplish red.

Section *Franciscea* has a much shorter tube that is only one to five times as long as the calyx. It is briefly inflated near the apex to include the anthers and stigma, then slightly constricted to form a raised, fleshy ring. The tube may be white or violet, and the limb is deep to pale violet, fading to pale lavender or pure white with age. The ring or eye at the center may be white or yellow. The limb in section *Franciscea* may be large and varies from 1.5 to 8 cm in diameter. The lobes are broadly rounded, overlapping at the lateral margins.

The corolla tube in section *Guianenses* is short, only two to three times as long as the calyx, and gradually dilated or inflated toward the apex. There is no marked constriction as in section *Franciscea*. The flowers in section *Guianenses* are white or greenish white and apparently do not change color with age. The corolla limb in section *Guianenses* is relatively small, rarely exceeding 25 mm in diameter. The lobes are quite narrow and convex; the lateral margins appear to be reflexed and are completely folded under in pressed specimens. This is also observed in *B. densifolia* of section *Brunfelsia* (Fig. 4).

The estivation of the corolla lobes in bud is a combination of quincuncial and imbricate. In quincuncial estivation, two of the lobes lie wholly to the outside, two wholly on the inside, and one lobe has one side to the inside and one to the outside. In section *Brunfelsia* the uppermost lobe is wholly to the inside, one of the lower lobes is wholly to the outside, and the other three are imbricate with one side in and one side out.

Only the size of the corolla and the shape of the lobes are useful as taxonomic characters. Within each section the corolla is quite similar. Characters such as color and the shape of the central eye in section *Franciscea* are diagnostic in the living state, but these are unfortunately lost in preparation of specimens and rendered useless to the herbarium taxonomist.

Androecium

The four stamens occur in two pairs in the upper part of the corolla tube, alternating with the

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FIG. 4. *Brunfelsia densifolia* (Knapp *s.n.*) from Puerto Rico.

upper three corolla lobes. A fifth stamen is occasionally produced in *Brunfelsia americana*, but this is an irregular condition. The glabrous filaments are fused to the corolla tube for most of their length and are free for only 2–5 mm. The anterior pair is longer, exceeding the stigma, and may be briefly exserted from the tube (*B. obovata*, *B. chocoensis*); the posterior pair, attached to the "back" of the tube, is shorter than the style. Both pairs are curved at the apex to project the anthers toward the back of the tube. In section *Brunfelsia* the filaments may be curved somewhat in the region of the stigma (*B. americana*, *B. lactea*).

The anthers are medifixed to the filaments and dehisce by a single longitudinal slit. In section *Brunfelsia* the anthers are oblong-reniform and may appear to be slightly bilobate, although the cells are confluent. At anthesis, each pair may tend to adhere to each other, apparently from the sticky nature of the pollen. *Brunfelsia densifolia* is somewhat anomalous in having both pairs of anthers reaching the mouth of the tube; the anterior pair is much reduced in size, although it produces a small amount of pollen. They are not completely sterile, as implied in Urban's original description (Krug & Urban, 1897). Slight inequality in anther size is not unknown in other species (cf., *B. martiana*) and hardly merits the formation of a new genus as proposed by Urban (1906). In sections *Franciscea* and *Guianenses* the anthers are unilocular and more or less semicircular, appearing round or reniform in outline.

Pollen

The pollen grains of all three sections of *Brunfelsia* are spheroidal.[3] Those of section *Brunfelsia* (*B. americana*, *B. undulata*) and section *Guianenses* (*B. chocoensis*, *B. martiana*) appear triporate or possibly tricolporate. Those of section *Franciscea* are tricolpate or tricolporoidate (*B. chiricaspi*, *B. grandiflora*, *B. latifolia*, *B. pilosa*). They are all medium-sized grains 30–38 to 34–42 μm in diameter.

The surface of the pollen was examined by means of a scanning electron microscope using unacetolyzed grains. These revealed low-relief scrobiculate or reticulate exine patterns. Although the sculpturing appears to differ slightly from species to species, the preparations were not sufficiently clear to permit a detailed analysis, nor were enough species observed to permit generalization.

[3] Pollen grains of *Brunfelsia* species were acetolyzed according to the procedure of Erdtman (1960).

Gynoecium

The ovary is ovoid or conical and is inserted on a short, nectar-producing disc that may be obscure in dried specimens or appear merely as a slight thickening at the base of the ovary. The ovary is bilocular with axile placentation, bearing numerous anatropous ovules. The thin dissepiments occasionally do not extend to the apex of the ovary, breaking down early in fruit formation and leaving the placenta attached only at the base. The fruit then may have only one locule.

The style is filamentous and nearly equals the corolla tube in length. It may be somewhat thickened and curved at the apex, especially in sections *Franciscea* and *Guianenses*, or suberect, as in several species of section *Brunfelsia*.

The stigma is usually included between the four anthers in the uppermost part of the tube. Only rarely does it project to the mouth of the tube (*B. densifolia*). The stigma is short and briefly bifid in sections *Franciscea* and *Guianenses* and faces the posterior wall of the corolla tube. It has the appearance of an open forceps at anthesis with the stigmatic tissue included between the lobes. After pollination, the lobes close together. In section *Brunfelsia* the stigma is more shallowly lobed and may appear subcapitate and convex.

Fruit

There has been considerable misinterpretation of the fruit of *Brunfelsia* from both a morphological and a phylogenetic point of view. This has occurred, I believe, because early botanists had very little material to work with and drew their conclusions from only a few specimens. The fruit varies considerably from group to group, and different fruit types may be found in otherwise closely related species. In some cases, the nature

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FIG. 5. *Brunfelsia lactea* (Knapp *s.n.*) from Puerto Rico.

of the pericarp and surface of the fruit may be important in differentiating species; fruit characters should be used whenever possible. Unfortunately, the fruits of many species are poorly or not at all known.

The fruit of *Brunfelsia* is essentially a capsule, not a berry as suggested by Miers (1850) and others in the past. There is, however, great variation in the texture of the pericarp, which may be thin-walled and brittle, leathery, fleshy or hard and indurated (bony). In shape it ranges from globose to ovoid, and in size, from 1 to 5 cm long. There may be two locules or only one by degeneration of the dissepiments. The surface may be smooth or rough; reticulate or areolate; and green, brown, or bright yellow or orange. The pericarp may be differentiated into three distinct layers or may be more or less fused into one. In all cases the endocarp is a thin, somewhat cartilaginous layer that on drying becomes brittle. The outer layers of the fruit wall often separate from the endocarp when the fruit rots. The thin endocarp may then split in half to release the seeds.

The uncertainty and controversy concerning the nature of the fruit in *Brunfelsia* (see "Ecology and Reproductive Biology") reflect the scarcity of fruiting material for many species. In reality, there is a wide spectrum of variation in the texture of the pericarp, which has led different authors to classify the fruit variously as a berry, a capsule, or a drupe. The fruits of certain species are indeed difficult to classify, demonstrating the limitations in our terminology. When the full range of forms is seen, however, it is clear that all the fruits of *Brunfelsia* are modifications of the capsule. Different types of capsule are found in each of the three sections of the genus, and no type is unique to any one section.

In section *Brunfelsia* the fruit is usually leathery or fleshy and brightly colored. The calyx persists only at the base. In *B. americana* and *B. densifolia*, the valves are fleshy and yellow and orange, respectively. The valves split apart at maturity in a true dehiscence (Fig. 6). *Brunfelsia jamaicensis* is green at maturity, with a thick, bony pericarp. *Brunfelsia maliformis* Urb. has a large, fleshy to leathery fruit with a distinct reticulate-areolate surface. It apparently does not open except by rotting. (*B. lactea* has orange valves that rot, allowing the seeds to be shaken out.—*Eds.*). Some of the Cuban species have fruits that are thin-walled, indehiscent, and usually brightly colored (*B. nitida*, *B. clarensis* Britton & P. Wilson). These may function as a berry in dispersal by animals.

In section *Franciscea* the fruit is usually a relatively small capsule that is green or brown and has a coriaceous pericarp that becomes thin and brittle on drying. The persistent calyx encloses the fruit, at least in part. These capsules may split open at maturity, but only sparingly. It may be that many species are completely indehiscent and their seeds are released only upon rotting on the forest floor. Two anomalous species are *B. dwyeri* (from Panama) and *B. macrocarpa* (from South America), in which the fruits have a leathery and a fleshy pericarp, respectively. The calyx of *B. macrocarpa* increases greatly in size and itself becomes fleshy, completely enclosing the bright yellow fruits.

In section *Guianenses* we find fleshy, yellow fruits in two of the six species, with the short calyx present only at the base. The fruits of *B. amazonica* and *B. burchellii* are thin-walled and dry at maturity; the fruit of *B. martiana* is as yet unknown.

Seed

The seeds are oblong or ovoid and often angular or compressed on one or more sides. They range in size from 2 to 13 mm long and in diameter from 1 to 7 mm. The surface texture is reticular-pitted and reddish brown in color. The surface pitting is formed by many tightly compressed surface outgrowths, resembling globulose hairs, that slough off as the seeds reach maturity. [See Souèges, 1907; Edmonds, 1983; Lester & Durands, 1984. These hairs are lignified thickenings of the lateral testal cell walls.—*Eds.*] Each of these hairs leaves a tiny pit in the surface. The embryo is relatively large and straight and is embedded in endosperm. The cotyledons are flat and ovate to elliptic. The size of the seeds may be useful as a taxonomic character, but their shape and number per capsule appear to be quite variable.

V. Cytology

The chromosomes of very few species of *Brunfelsia* have been investigated. Four counts for the genus are known from the literature, but these are of limited value at the specific level because no voucher herbarium specimens were prepared.

FIG. 6. Fruit of *Brunfelsia americana*.

TABLE 2. Chromosome counts in *Brunfelsia*.

Species	Chromosome no.	Author
B. americana	$2n = 22$	Bhaduri (1933)
B. americana	$n = 11$	Madhavadian (1968)
B. australis	$n = 12$	Ratera (1944)
B. calycina (= *B. pauciflora*)	$2n = 22$	Darlington and Janaki Ammal (1945)
B. dwyeri	$2n = 22$	Davidse (1981)
	$2n = 22$	Bhaduri (1933)
B. americana	$n = 11$	Madhavadian (1968)
B. australis	$n = 12$	Ratera (1944)
B. calycina (= *B. pauciflora*)	$2n = 22$	Darlington and Janaki Ammal (1945)
B. dwyeri	$2n = 22$	Davidse (1981)

These findings are summarized in Table 2. On the basis of this evidence, Darlington and Wylie (1955) hypothesized that the base number for *Brunfelsia* is $x = 11$.

The mitotic chromosomes of *Brunfelsia* are difficult to prepare because the young root tips produced in flower pots tend to be hard and brittle, making squashes very difficult. Treatment in 1% HCl softens the material somewhat, but despite this treatment, no good mitotic figures could be found in three species examined (*B. australis*, *B. latifolia*, *B. pauciflora*). Sufficient seeds of *Brunfelsia* were not available to test the possibilities of preparing squashes from the roots of young seedlings.

A second method of obtaining chromosome preparations is to examine pollen mother cells undergoing meiosis. Young flower buds were collected both in the field and from cultivated specimens in the greenhouse and immediately placed in Carnoy's solution for at least 24 hr and refrigerated when possible. Material was collected about midday on sunny days. It was difficult to obtain a sufficient number of buds because brunfelsias generally have few flowers per inflorescence, and these are usually in various stages of maturation; not infrequently only one flower per inflorescence per day will be available for cytology. Compounded by the fact that most species flower only sporadically and some not at all under greenhouse conditions, securing adequate material was a task.

Meiosis occurs in *Brunfelsia* when the buds are very small (about 1.0–2.5 mm long) and well before the corolla emerges from the calyx. The young anthers were teased out in 2% acetocarmine and gently heated, then squashed with even pressure. Relatively few countable meiotic figures were obtained out of numerous attempts. The results obtained in five species and one subspecies are summarized in Table 3.

All counts were obtained from meiotic figures with the exception of *B. pauciflora*, which apparently represents a somatic division in a tapetal cell. The meiotic figures obtained were fixed in late anaphase I or telophase II. The chromosomes are small, from 2.0 to 5.5 μm (cf., Swanson, 1957), and exhibit some size variation between the different species examined. In the case of *B. nitida* and *B. americana*, the smaller size is due to the fact that only two chromatids are present (telophase II). The somatic chromosomes of *B. pauciflora* appear greatly enlarged. This is probably the result of endomitosis, which produces a high degree of endopolyploidy within the cell. Unfortunately, no normal mitotic cells could be obtained for this species.

The chromosomes obtained from these species were very compact in the stages observed, suggesting a high degree of contraction due to chromosomal coiling. No details of chromosomal structure could be ascertained from the meiotic figures. It is possible, however, to see the centromere in the somatic chromosomes of *B. pauciflora*.

In an extensive investigation, Gottschalk (1954) examined the structure of the pachytene chromosomes of many species of Solanaceae, with particular reference to the presence and position of heterochromatic and euchromatic areas. Because of the high degree of contraction, he was unable to obtain pachytene chromosomes in what he referred to as *B. macrophylla* (probably *B. pauciflora*). He did, however, observe the presence of chromocenters in the interphase nucleus, indicating that the chromosomes of this genus are differentiated into euchromatic and heterochromatic regions. Similar results were found in species in

TABLE 3. Chromosome numbers and size in *Brunfelsia*.

Species	Chromosome no.	Voucher	Origin	Division	Stage	Length (μm)	Width (μm)
B. grandiflora ssp. *grandiflora*	$n = 11$	Plowman 2960	Miami, Fla.	Meiotic	Late anaphase I	3–3.5	2–2.5
B. grandiflora ssp. *schultesii*	$n = 11$	Plowman 2404	Colombia	Meiotic	Late anaphase I	3–4	2–2.5
B. pauciflora	$2n = 22$	Plowman 3392	Woburn, Mass.	Mitotic	Metaphase	4.5–5.5	3–4
B. latifolia	$n = 11$	Plowman 3353	Woburn, Mass.	Meiotic	Late anaphase I	3–3.5	2–2.5
B. nitida	$n = 11$	Plowman 1904	Venezuela	Meiotic	Telophase II	2–2.5	1.5
B. americana	$n = 11$	Plowman 1903	Venezuela	Meiotic	Telophase II	2–2.5	1–1.5

related genera (*Browallia grandiflora sensu* Gottschalk (1954) (probably *B. speciosa* Hook.) and *Nierembergia coerulea* Gill. ex Miers).

From the preliminary results obtained in this study, it may now be safely predicted that the base chromosome number in *Brunfelsia* is $x = 11$. Ratera's (1944) count of $n = 12$ in *B. australis* was not confirmed because no flowering material was available for this species. This count, however, should be repeated at the earliest possible opportunity. Both section *Brunfelsia* and section *Franciscea* have 11 pairs. No material from section *Guianenses* was available.

The most common chromosome number for the Solanaceae is $2n = 24$. There has been considerable debate about whether it can be assumed that 12 pairs represent the base number for the family. Goodspeed (1954) presented evidence that the primitive number for the family may be six pairs ($2n = 12$), from which higher numbers were derived by secondary association.

Related genera of the tribe Salpiglossideae have various chromosome numbers. Four genera (*Streptosolen*, *Salpiglossis*, *Browallia*, *Brunfelsia*) have 11 pairs ($2n = 22$). Lower numbers occur in *Petunia* ($2n = 14$), *Nierembergia* ($2n = 18$), and *Schizanthus* ($2n = 20$). The endemic Australian genus *Duboisia* has 30 pairs ($2n = 60$) (Darlington & Wylie, 1955; Madhavadian, 1968).

The Salpiglossideae are thought to be derived, at least in part, from the Cestreae, in which tribe the following chromosome numbers have been derived: *Cestrum* L. and *Vestia* Willd., eight pairs ($2n = 16$); *Fabiana* Ruiz and Pavón, nine pairs (2n = 18); and *Nicotiana* L., eight, nine, ten, 12, 18, 19, 20, 21, and 24 pairs, which represents a well-known aneuploid series (Goodspeed, 1954). Because the cytology of several important genera, such as *Juanulloa* Ruiz and Pavón, *Markea* Rich., and *Sessea* Ruiz & Pavón of the Cestreae and *Anthocercis* and *Anthotroche* of the Salpiglossideae, have not been studied, it would be risky to draw any phylogenetic conclusions on the basis of chromosome number alone. It seems reasonable, however, to suggest that *Brunfelsia* and other genera of the Salpiglossideae originated from an ancestral 12-paired precursor through aneuploidy.

VI. Hybridization Experiments

As an aid to investigating the breeding systems and interspecific relationships in *Brunfelsia*, a pro-

gram of artificial hybridization was undertaken. Plants obtained from both wild and cultivated sources were grown at the Biological Laboratories Greenhouse, Harvard University, and at Northeastern University Greenhouses in Woburn, Massachusetts.

There are several inherent difficulties in attempting artificial hybridization in woody perennials such as *Brunfelsia*. Although germination is relatively rapid, the time required from seed to flower varies from a minimum of 6 months to several years. In *Brunfelsia* flowering may be sporadic or rare under greenhouse conditions, and in most species only a few flowers per plant are open at any one time.

Seventeen clones, representing ten species of the genus, were available for making crosses, including five each from section *Franciscea* and section *Brunfelsia*. Other species were grown but could not be induced to flower. A major problem in making crosses was the lack of simultaneous flowering in desired species. Some species (*B. americana*, *B. pauciflora*) flowered almost continuously throughout the year; others flowered only occasionally or not at all. Attempts to store pollen under refrigeration for future crosses were unsuccessful.

Pollination was accomplished by excising the corolla limb and uppermost part of the tube to expose the anthers and pistil. Pollen was then transferred using a small brush. The anthers usually dehisce before the complete unfolding of the corolla lobes and scatter the pollen on the inside of the tube. The stigma is receptive just before the flower opens and remains so for 2–3 days.

Because of the small number of plants available, the results of the breeding experiments were generally inconclusive. The majority of crosses made, whether inter- or intraspecific, produced no fruit. The flowers withered and persisted (*B. americana*, *B. australis*) or dropped off in 1–3 days (*B. densifolia*, *B. lactea*, *B. pauciflora*).

The data obtained from the breeding program are summarized in the following paragraphs. The actual records of the crosses are not included because they are lengthy and, for the most part, negatively repetitious. The following species were included in the program: *B. americana*, *B. australis*, *B. densifolia*, *B. grandiflora*, *B. lactea*, *B. latifolia*, *B. nitida*, *B. pauciflora*, *B. pilosa*, and *B. undulata*. Reciprocal crosses were made between these where possible.

All species were artificially self-pollinated, although selfing appears to take place naturally. The dehiscing anthers lie very close to the stigma, and loose pollen may easily fall upon it. However, no viable seed was produced from any of the self-pollinated individuals, indicating that these species are self-incompatible. Fruits were occasionally produced spontaneously in *B. pilosa* and *B. densifolia*, but these contained completely aborted seeds.

Mature fruit containing viable seeds was produced in the following intraspecific crosses between nonclonal individuals within the following species: *B. latifolia* × *B. latifolia*, *B. pauciflora* × *B. pauciflora*, *B. americana* × *B. americana*, and *B. densifolia* × *B. densifolia*. However, even in these species many of the crosses did not take or produced aborted or hollow seeds. This may be attributed to various factors. In some cases failure to set seed may have been due to fluctuations in greenhouse conditions or the use of certain pesticides. Certain plants (*B. americana*, *B. pauciflora*) were of cultivated origin and may have been clones of individuals highly selected for ornamental characters; reproductive irregularities are not uncommon in these forms. Lastly, these failures may have been the result of innate incompatibility factors as yet uninvestigated in the genus.

The failure of interspecific crosses suggests that all the species investigated are reproductively isolated. In one case this may be significant in view of specific delimitation. No viable seeds were produced in crosses between *B. australis* and *B. pilosa*, two species of southern Brazil that were formerly considered conspecific with *B. uniflora*.

This lends support to the view that *B. australis* and *B. pilosa* should be considered distinct species. Additional crosses involving these two species as well as *B. uniflora* would be useful in confirming and further clarifying the relationships among them.

VII. Ecology and Reproductive Biology

Habitat

Brunfelsia species are found in a variety of habitats. Species of section *Brunfelsia* of the Antillean region are frequently encountered in rocky woodlands or thickets on limestone (*B. laliformis*, *B. membranacea*, *B. splendida*) or serpentine soils (*B. densifolia*, *B. shaferi* Britton & P. Wilson, *B. sinuata*), often in relatively dry situations. Oth-

er species grow in humid, montane rain forests (*B. portoricensis*) and in cloud forests at higher elevations (*B. lactea*, *B. jamaicensis*). Most of the species of this section are limited in ecological tolerance and restricted to relatively small and local areas. Only *B. americana*, which also has the widest ecological amplitude, occurs on more than one island (see Appendix II for a list of species in section *Brunfelsia* and their distributions).

The basic ecology of section *Brunfelsia*, particularly the Cuban species, is virtually unknown. As in the case of many plants of limited distribution, many of the Antillean species are now in grave danger of extinction because of the destruction of their habitats. Several species in Jamaica are known from a few local populations (e.g., *B. jamaicensis*, *B. membranacea*, *B. plicata*, *B. splendida*) that are rapidly being encroached upon by human activities. The only known wild population of *B. undulata*, on the north coast of Jamaica, was recently eliminated by the construction of a cattle path. *Brunfelsia picardae* Krug. & Urb. of Haiti has not been collected since 1928. Little is known of the many Cuban endemics, the majority of which are rare and known from only one or a few collections.

The three Puerto Rican endemics are currently protected from man's destruction because they are now all included within the boundaries of national parks. However, the only known population of *B. americana* in Puerto Rico is precariously located in a pasture near Coamo.

If the incredible increase in human population in the West Indies continues at its present rate, the sheer pressure of human needs will surely lead to destruction of the few remaining natural areas. Many of the Antillean species of *Brunfelsia* have large, showy flowers of potentially great horticultural value. Several of these have already been successfully introduced into cultivation (*B. americana*, *B. nitida*, *B. undulata*), but the remainder are in danger of being lost completely. In addition, several of these plants have been shown to contain alkaloids or to be of interest medicinally. In this study, an effort was made to distribute seeds and cuttings of as many wild species as possible to tropical botanical gardens and conservatories to preserve them in cultivation.

The six species of section *Guianenses* all grow in low-elevation tropical rain forests in continental South America; they are found in the shrubby stratum of the understory and at the margins of rivers. Species of this group have not been studied in the field, and little is known of their biology. They are mostly known from only a few collections.

The South American species of section *Franciscea* are primarily shrubs or small trees of the understory of humid tropical rain forests; those species that have adapted to other environments are considered more specialized. This group grows primarily in mountainous regions, up to about 2,000 m of altitude. Exceptions are found in several species that appear to be restricted to very low elevations (*B. australis*, *B. imatacana* Plowman, *B. latifolia*, *B. macrocarpa*) and in *B. uniflora*, which reaches 3,300 m in the Bolivian Andes.

A number of species of section *Franciscea* have become specialized in their ecological requirements. *Brunfelsia latifolia* grows only on sandy *restingas*, a maritime formation of low shrubs on the coast of southeastern Brazil. *Brunfelsia obovata* is adapted to semiaquatic environments and grows in marshes (*brejos*), often in standing water, or along flooded river margins from southeastern to central Brazil. In southern Brazil, *B. cuneifolia* and *B. pilosa* are restricted more or less to the region of the *Araucaria* forests of Paraná, Santa Catarina, and Rio Grande do Sul, and *B. rupestris* grows only in the *campo rupestre* habitat of the Serra do Espinhaço in Minas Gerais, Brazil. *Brunfelsia australis*, the southernmost species of the genus, grows in gallery forests and in small patches of woodland found on raised ground in the low-lying Paraná River basin.

Two species have a wider ecological amplitude and are found in varied habitats, including secondary forest growth and disturbed areas. *Brunfelsia brasiliensis* grows in the humid forests of Rio de Janeiro, especially in well-drained sites such as outcrops and rocky peaks. It also flourishes in the drier mountainous states of Minas Gerais and São Paulo, often persisting in secondary growth woodlands and in gallery forests. *Brunfelsia uniflora* is a wide-ranging species that occurs in the rain forests of the Serra do Mar; in the drier central and northeastern states of Brazil; on the dry coast of Venezuela, and, lastly, in the high-altitude cloud forests of the Bolivian Andes. This is perhaps the most widespread species in Brazil because of its ability to survive in disturbed habitats.

Certain species of sections *Franciscea* and *Guianenses* are of such local occurrence that they may also be considered endangered. This is particularly true of *B. latifolia*, which is precariously restricted to the region around the city of Rio de

Janeiro, and of *B. dwyeri*, on the upper slopes of Cerro Jefe in central Panama. Both of these areas are rapidly being developed for housing and farming, respectively. A large portion of Cerro Jefe has already been decimated for building poultry farms. Little is known of the effect of human activities on other South American species because they have not been studied in the field. The danger of their extinction is less serious, however, than for the West Indian species because of the usually wider distribution of the continental species.

Life Cycle

The seeds of *Brunfelsia* species germinate within 2–4 weeks of planting and are relatively short-lived. They will not tolerate desiccation. Most species are slow-growing woody shrubs that vary in the time required to mature from seedling to flowering plant. Under greenhouse conditions plants mature from 6 months (*B. latifolia*) to 2 or more years after germination. Several species are known to flower while the plants are still small, even though they may eventually become trees in nature. Little is known about the longevity of individual plants, but there is evidence that they grow for at least 20 years (*B. grandiflora*). Vegetative reproduction may also occur to a limited extent by the rooting of broken branches on the forest floor. This has been observed in *B. chiricaspi* (*Plowman 2081*).

The flowering period in *Brunfelsia* may be short, lasting only a few weeks, or extend more or less continuously throughout most of the year. Flowering specimens have been collected from the type locality of *B. grandiflora* subsp. *schultesii* in January, May, and September. The majority of the South American species flower between October and December.

The fruits of *Brunfelsia* require several months to a year for ripening and may remain on the plant even after the seeds are fully mature, until the fruits are dried and brown. Dehiscence of the fruits is discussed under "Dispersal Mechanisms."

Pollination Biology

The flowers of *Brunfelsia* are well adapted for insect pollination, specifically by moths and butterflies. No other kinds of insects have been observed to visit the flowers. The three basic forms of the corolla found in the genus have apparently evolved through selection for specific groups of pollinators: section *Franciscea* for butterflies, section *Brunfelsia* for hawk moths, and section *Guianenses* probably for other moths [or perhaps bees—*Eds.*]. All the species have a disc at the base of the ovary that secretes abundant nectar in the base of the tube. So far as is known, they are all self-incompatible.

Species of section *Franciscea* have flowers with a relatively short tube and a brilliant violet limb with a white eye at the throat, which presumably serves as a nectar guide. The somewhat raised, fleshy rim at the throat may function as a landing platform for the visiting insect. The violet color of the flower fades to pale lavender or pure white with age and may signal the insect that the flowers are no longer receptive. The flowers are rarely scented in this group, although two species (*B. australis*, *B. imatacana*) are exceptionally fragrant with a scent resembling that of jasmine.

Butterflies in four different families have been collected on the flowers of *B. grandiflora*, including species of *Euptychia* (Nymphalidae), *Eurema* (Pieridae), *Euselasia* (Lycaenidae), and the *Calpodes* group (Hesperidae) (see Table 4). In southern Colombia the most frequent visitor of these was an unidentified species of *Euptychia*.[4]

Species of *Brunfelsia* sect. *Brunfelsia*, in contrast, possess a much longer corolla tube than those of section *Franciscea*. They are usually white upon opening and fade to yellow with age. They bloom at night and are highly perfumed, beginning to produce scent just before sunset. The fragrance of a few flowers is capable of pervading a relatively large area of forest. These flowers have no landing platform as found in section *Franciscea*, which suggests that the insect hovers while feeding.

Although no insect pollinators have been seen on the flowers of the Antillean species, these are typically pollinated by moths. In view of the length of the corolla tube (up to 14 cm), it may be said with some certainty that hawk moths (Sphingidae) are responsible for pollination in this group. Similarly constructed, fragrant white flowers in other families of plants are known to be pollinated by hawk moths, such as *Ipomoea alba* Garcke (Convolvulaceae), *Aquilegia longissima* A. Gray (Ranunculaceae), *Habenaria leucophaea* A. Gray (Orchidaceae), *Hippobroma longiflora* G.

[4] Identified by Prof. John Burns, Museum of Comparative Zoology, Harvard University.

TABLE 4. Pollinators of *Brunfelsia grandiflora*.

Family	Subfamily	Genus	Voucher	Locality
Subspecies *schultesii*				
1. Nymphalidae	Satyrinae	*Euptychia* sp. 1	Plowman 2091	Putumayo, Colombia
			Plowman 2533	Loreto, Peru
2. Nymphalidae	Satyrinae	*Euptychia* sp. 2	Plowman 2533	Loreto, Peru
3. Nymphalidae	?	?	Plowman 2091	Putumayo, Colombia
4. Pieridae		*Eurema* sp.	Plowman 2091	Putumayo, Colombia
5. Lycaenidae	Riodininae	*Euselasia* sp.	Plowman 2533	Loreto, Peru
Subspecies *grandiflora*				
6. Hesperidae	Hesperiinae	*Calpodes* group	Plowman 2912	Rio de Janeiro, Brazil
7. Hesperidae	Hesperiinae		Plowman 2912	Rio de Janeiro, Brazil

Don (Campanulaceae), and species of *Randia* L. (Rubiaceae), *Quisqualis* L. (Combretaceae), and *Brugmansia* Pers. (Solanaceae).

The pollinators of section *Guianenses* are not known. The flowers in this group have a short tube but are white and have no landing platform; both *B. amazonica* and *B. chocoensis* are reputed to be fragrant, suggesting that they may also be pollinated by moths. This remains to be confirmed in the field.

Dispersal Mechanisms

The fruits of *Brunfelsia* are basically capsular and of two general types: a more or less thin-walled capsule that becomes dry and brittle with age or a more or less thick-walled capsule, the valves of which may be fleshy, leathery, or bony at maturity. Both types of fruit occur in all three sections of the genus.

The fruits of most species of *Brunfelsia* do not dehisce to release the seeds as is common in most capsules; at best they are tardily dehiscent. They frequently remain on the plant well after the seeds are ripe, becoming dry and brown, in which state of brittleness they may then break apart on the plant [but see discussion of fruit types in *Solanum* in Symon (1979)—*Eds.*]. Alternatively, the whole capsule may fall to the ground, where the outermost layer of the pericarp rots away, leaving the thin, brittle endocarp. This eventually breaks in half along the lines of dehiscence to release the seeds.

Most of the South American species of *Brunfelsia* have capsules that are green or brown at maturity and included in the dark green calyx. As a result, the fruits are very inconspicuous; fruiting specimens are almost never collected. In the absence of any pronounced color, odor, or edible flesh, it seems unlikely that the fruits could be attractive to animals. These species apparently have no special adaptations for dispersal, a situation that has been pointed out for many shrubs and trees of the primary rain forest (Richards, 1952).

The thin-walled, capsular species may be dispersed over short distances by water. The air spaces created by placental breakdown and the lack of dehiscence permit these fruits to float. After they have fallen to the ground, they may be carried away from the parent plant during heavy rains, especially along river courses.

Other species in South America and in the West Indies have rather large, orange or yellow fleshy fruits that are probably dispersed by birds or mammals. Examples of these are *B. chocoensis*, *B. densifolia*, *B. guianensis*, *B. macrocarpa*, and *B. nitida*. Two of these (*B. chocoensis*, and *B. macrocarpa*) are said to be edible and probably have a sweet flesh that would attract animals. However, animal dispersal has not been observed in the field.

Plant–Insect Relationships

In addition to pollinators, other insects are intimately associated with the genus *Brunfelsia*. One of the most interesting is the butterfly genus *Methona* (Rhopalocera, Nymphalidae), the larvae of which feed exclusively on the leaves of *Brunfelsia* species. This and related groups have been studied by Dr. Gerardo Lamas of the Museo de Historia Natural, Lima, Peru (Lamas, 1973).

Methona (Fig. 7) is a genus of medium-sized butterflies (wing span of 7–10 cm) consisting of seven species and nine subspecies. The larvae are

FIG. 7. *Methona themisto* (type specimen at BMNH).

gregarious and warningly colored (Fig. 8). The species of *Methona* are all tropical forest insects and are distributed in the same areas of South America where *Brunfelsia* occurs. The greatest concentration of *Methona* species is found in the Andes; three species occur in the Amazon basin, two occur in northeastern Brazil, and one occurs in southeastern Brazil. A disjunct population, considered a distinct subspecies of *M. confusa*, lives only on Cerro Jefe in Panama (Lamas, 1973).

Until the present, the documentation of the *Brunfelsia–Methona* relationship has been patchy, primarily because of the lack of voucher specimens of the host plants. Larvae of *M. themisto megisto* have been collected on *B. australis* in Misiones Province of northeastern Argentina (*Plowman 2731*) as well as in Buenos Aires and Uruguay. Reports from the latter two sites were made from cultivated plants that were incorrectly identified as *B. pauciflora*, *B. uniflora*, and *B. latifolia*, even though none of these species are known this far south in the wild or in cultivation. The same species of *Methona* has been collected in Tucumán in western Argentina. Although no species of *Brunfelsia* occurs there naturally, *B. australis* is cultivated in gardens and must serve as the host.

Other species of *Methona* have also been found on *Brunfelsia* species: *M. singularis* in Paraíba in northeastern Brazil and *M. confusa confusa* in Manaus in the Amazon basin. Without voucher specimens, it is difficult to say which species of *Brunfelsia* were involved.

The geographical distribution of *Methona* exhibits a striking parallel to that of the South American brunfelsias. The butterfly, however, does not

→

FIG. 8. Caterpillars of *Methona confusa* on leaf of *Brunfelsia chiricaspi*.

TABLE 5. *Brunfelsia* species recorded as larval food plants for species of *Methona* (Lepidoptera: Nymphalidae: Ithomiinae).

Species	*M. confusa*	*M. megisto*	*M. singularis*	*M. themisto*
B. amazonica	•			
B. australis				•
B. dwyeri	•			
B. grandiflora	•	•		
B. pauciflora	•			•
B. mire		•		
B. martiana		•		
B. uniflora			•	•

occur in the West Indies, suggesting that it arose in South America after *Brunfelsia* sect. *Brunfelsia* became cut off from its South American ancestors. Not enough data are available at the present time to indicate whether there may be any species-specific relationships between *Brunfelsia* and *Methona*. A summary of the species of *Brunfelsia* fed upon by the larvae of *Methona* is presented in Table 5 [more detailed information can be found in Drummond and Brown (1987)—*Eds.*].

The capsules of *Brunfelsia* species in South America are also fed upon by Lepidopteran larvae. The flesh of the young fruit and the seeds are eaten by tiny larvae[5] of the family Gelechiidae. These have been found in the following species: *B. australis* (*Plowman 2723*), *B. brasiliensis* subsp. *macrocalyx* (Dusén) Plowman (*Plowman 2891, 2906*), and *B. grandiflora* subsp. *schultesii* (*Plowman 2404*). Further identification of the insects has not been possible. They apparently lay their eggs on or near the developing fruits. The larvae then burrow through the pericarp and devour the seeds and placental tissue.[6]

Protection from this predation may be the origin of certain specializations in the genus. The fruits of several species (*B. macrocarpa*, *B. hydrangeiformis*, *B. pauciflora*) are completely enclosed in the often coriaceous calyx, which may offer some defense against the insect larvae. The thick, leathery valves in the capsules of *B. dwyeri* may serve a similar function.

A third insect–plant relationship has been observed in southern Colombia in *B. grandiflora* subsp. *schultesii*. Two species of ants[7] in the genera *Campanotus* (Formicinae) (*Plowman 2416*) and *Pheidole* (Myrmicinae) (*Plowman 2151*) form temporary bivouacs among the fruit clusters of the plants. Associated with the ants are two different Homopteran insects (one in the family Psillidae, the other unidentified) that feed on the plant and apparently are tended by the ants. *Pheidole* manufacture a nest of "carton" (cellulosic material) among the fruits that may serve to protect their charges. This may represent a symbiotic relationship between the ants and Homopterans, but it is not clear what advantage, if any, this may give to the plant.

VIII. Trends in Specialization

In attempting to understand the evolutionary relationships among the sections and species of *Brunfelsia*, it is necessary to determine which characters are primitive or unspecialized and which are derived and specialized. Levels of specialization may be observed in several organs of the plants, including leaves, flowers, and fruits, as well as in habitat preferences and other ecological factors. Because the species of section *Brunfelsia* have not been studied in depth, the following discussion is limited primarily to the South American species of section *Guianenses* and section *Franciscea*.

Of the South American brunfelsias, the flowers of section *Guianenses* are the least specialized and possibly ancestral to section *Brunfelsia*. The corolla tube is short in section *Guianenses* and open at the mouth with relatively narrow corolla lobes. The corolla is white or greenish white, suggesting pollination by moths.

Section *Guianenses* occurs primarily in the Amazon basin with disjuncts in Chocó and Bahía. There is a distinct tendency in this group toward axillary, few-flowered inflorescences on the older branchlets, although terminal flowers are also produced. Two species (*B. chocoensis*, *B. guianensis*) have capsules with fleshy valves, and two others (*B. amazonica, B. clandestina*) have a dry, thin-walled capsule. The fruit of the remaining two species (*B. martiana*, *B. burchellii*) is unknown. Evolution in the type of fruit, however, shows no

[5] Identified by Dr. Donald Duckworth, U.S. National Museum, Washington, D.C.

[6] The taxon-specific relationships between members of the Gelechiidae and other Solanaceae have been well-documented in the temperate zone but not in the tropics (see Foott, 1967; Scholtz, 1978; Solomon & McNaughton, 1979)—*Eds.*

[7] Identified by Prof. E. O. Wilson, Department of Biology, Harvard University.

overall direction because different types of fruit (dry vs. fleshy, etc.) have probably arisen repeatedly under local selection pressures.

Section *Guianenses* is a small group that occurs in a relatively uniform environment with few major differences separating the species. It is therefore not surprising that trends of specialization are difficult or impossible to detect within the group.

Section *Franciscea* apparently arose as a section by becoming isolated in the Andean region, where the flowers coevolved with butterflies. The flowers are bright purple or violet with a distinct white or yellow eye. The corolla tube is short and somewhat constricted at the apex into a thickened ring. The limb is often large and showy with broad, rounded lobes.

The inflorescence of section *Franciscea* varies from a many-flowered, lax or compact cyme to a solitary terminal flower. Most of the species bear a few-flowered terminal cyme; the number of flowers per inflorescence may vary considerably in a single species (see "General Morphology").

Evolution in the inflorescence must first of all be considered in terms of the entire plant and pollination strategy. Species with several to many flowers in the inflorescence tend to have fewer flower-bearing branches (*B. chiricaspi*, *B. hydrangeiformis*, *B. mire*). Species with only one to three flowers are generally more profusely branched, with many of the branchlets bearing flowers (*B. australis*, *B. cuneifolia*, *B. uniflora*). In the first case, the flowers are aggregated into a large single mass (see Fig. 30); in the second, the entire shrub may be diffusely covered with many single flowers (see Fig. 45). Both modes of organization must be equally attractive to pollinators, although there may be different butterflies associated with the different forms of inflorescence. This association, however, has not been observed.

There is also a tendency for the one-flowered species to have larger flowers (*B. macrocarpa*, *B. pilosa*). Among the species with several (one to ten) flowers, there are many intermediate situations with respect to the number of flowers per branch, the number of branches, and the size of flowers. In adapting to local ecological conditions, available pollinators, etc., the species of section *Franciscea* have evolved a mosaic pattern of inflorescence organization within which these general trends can be perceived.

Attempts to ascertain the "primitive" condition of the inflorescence, i.e., whether it may have been one-, few-, or many-flowered, branched or unbranched, etc., leads to several problems. In terms of flower and fruit characters, two species appear to be least specialized, namely *B. uniflora* and *B. grandiflora*. Both of these occur in the Andean region, as well as in eastern Brazil, indicating, as shown below [and in Plowman (1979)—*Eds.*], that both species are relatively old for the genus. However, *B. uniflora*, as its name suggests, has but a single flower terminating the branch; *B. grandiflora* may have few to many flowers in a more or less branched inflorescence. We cannot, therefore, decide which of these may have a more primitive inflorescence solely on the basis of associated characters.

There has been considerable controversy over the origin of inflorescence types in the Angiosperms (for discussion see Constance, 1955; Lawrence, 1965). According to Lawrence, the inflorescence is a branch system in which a solitary flower is the terminal unit of each branch. Some workers believe that this single terminal flower is the primitive inflorescence from which more complex forms were derived through increased lateral branching. Others, including Rickett (1944), whose views have been widely repeated, interpreted the sequence in the opposite direction. Rickett considered the primitive condition to be a compound, branched inflorescence, specifically a compound dichasium, from which few- or solitary-flowered inflorescences were derived through suppression of lateral branches. He derived various inflorescence types, including the cincinnus, by reduction and condensation of the branch system. The solitary- or two- to three-flowered cyme could easily be derived from the cincinnus by mere suppression of the lateral branchlets. Accordingly, Lawrence concluded that "the modern or present-day inflorescence represented by a solitary flower in almost all plants is a product of reduction, a reduction that may have resulted from any one of many multiflowered inflorescence types, whose origin may be indicated only by comparative studies of inflorescences of related taxa."

One genus in the Solanaceae has been thoroughly studied from this point of view. Goodspeed, in *The Genus Nicotiana* (1954), postulated that an open paniculate inflorescence (a broad thyrse) is primitive in this group, from which a wide array of inflorescences has been derived, including glomerules and false racemes.

In conclusion and with reservations, I would designate the pluriflorous, branched inflorescences of *B. grandiflora* as the probable ancestral type for section *Franciscea*, from which fewer-flowered forms such as *B. bonodora* (Vell.) J.F.

Macbr. and *B. uniflora* have been derived by reduction. Condensed, many-flowered inflorescences such as are found in *B. mire* and *B. hydrangeiformis* could easily be derived from that of *B. grandiflora* by a shortening of the axis with a concomitant increase in the number of lateral branches.

Specializations in the calyx of *Brunfelsia* have occurred both between and within the sections. In section *Brunfelsia* the calyx is usually small and in fruit appears only at the base. The same is true of section *Guianenses* with the exception of *B. amazonica* and *B. clandestina*, in which the calyx partially encloses the thin-walled fruit. In section *Franciscea*, the latter situation is the rule: the calyx persists tightly appressed to the developing fruit, enclosing only the lower half of the fruit (*B. australis*, *B. grandiflora*) or far exceeding it in length (*B. hydrangeiformis*, *B. pauciflora*). Even in the fleshy-fruited members of this section (*B. macrocarpa*, *B. dwyeri*), the calyx envelops the fruit and in the former species becomes very large. The calyx in these species remains attached to the fruit when it falls from the plant.

The relative length of the calyx at anthesis varies considerably both within species (*B. brasiliensis*) and among them. However, a longer calyx in relation to the corolla tube indicates increased specialization, possibly as protection against robber bees or other insects that lance the base of the corolla tube to obtain nectar. Another feature of the calyx that is considered derived is the inflated and five-angled condition found primarily in *B. boliviana*, *B. cuneifolia*, and *B. obovata*.

The characters of the corolla were discussed above. The corollas of each of the three sections are distinctive, as demonstrated above, but show little variation or evolution within each section. However, minor differences do occur. In section *Brunfelsia* there has been some differentiation in the size of the corolla limb relative to the tube and in the color of the corolla. In section *Franciscea*, although somewhat variable in size and to a lesser degree in color, the corolla is relatively uniform, as it also is in section *Guianenses*.

Equally conservative is the form and relative size and position of the stamens and pistil. Within each section, there has been apparently little change. A tendency toward exsertion of the uppermost pair of anthers has arisen convergently in all three sections, but the adaptive significance of this, if any, is not known.

Several different types of fruit are found in the genus *Brunfelsia* and are distributed in all three sections. These have been classified variously as dehiscent or indehiscent berries; as fleshy, leathery, or dry capsules; or as drupes. After examining most of the species for which fruits are known, I would suggest that the basic or primitive fruit in the genus is a tardily dehiscent capsule with leathery valves. This basic form has undergone several modifications in response to particular environmental conditions and selection pressures for dispersal.

One of the most generally encountered derived characters is the loss of dehiscence, which may be partial or complete, in both thin- and thick-walled types. However, in many species, and especially in section *Franciscea*, the septicidal sutures (lines of dehiscence) remain on the fruit. There may be two additional sutures that divide the valves, apparently a vestige of previous four-way dehiscence. This mechanism is seen today in capsules of other genera in the Salpiglossideae, such as *Salpiglossis*, *Browallia*, and *Streptosolen*, as well as in *Nicotiana* and *Sessea* of the Cestreae. In *Brunfelsia dwyeri* the sutures are cruciform and prominently indented in the surface of the fruit. A septicidal line of dehiscence is readily observed in the endocarp of many species, which is usually cartilaginous and brittle on drying. As the mature fruit rots, the endocarp, which is often more durable than the mesocarp, remains and eventually breaks along the sutures through the agencies of weathering and predation. This I believe to be a vestige of the ancestral capsular form.

It is of interest here to compare the view of other workers in the field of Angiosperm evolution. Hutchinson (1969) believed that there is a general morphological trend within the Angiosperms in which the capsule has preceded the berry and drupe. Corner (1964), in summarizing his "Durian Theory," stated that "the primitive fruits of flowering plants were dehiscent arillate carpels or, in the syncarpous ovary, capsules. These fruits had bright red or orange walls and black seeds covered with red or orange edible arils." From this original type he derived the dry capsule with dry seeds, indehiscent types that led eventually to the fleshy berry, and the stone fruits and nuts by lignification of part or all of the fruit wall.

Similar trends can be readily observed in the Solanaceae operating at various taxonomic levels, including tribe, subtribe, genus, and species. The family is characterized by two main fruit types, the berry and the capsule. Both types occur in four of the five tribes of Wettstein (1895). The

fifth tribe, represented solely by *Nicandra*, bears a "dry berry."

Besides *Brunfelsia*, other genera show heteromorphism in their fruits. The genus *Lycium*, monographed by Hitchcock (1932) and pointed out by Croizat (1962), has mostly fleshy, tomato-like berries except in two species, *L. ameghinoi* Spegazzini and *L. californicum* Nutt., which bear capsules. An anomalous species, *L. macrodon* A. Gray, has a curious intermediate type of fruit.

A second example is found in the genus *Cestrum* and its close relative *Sessea*. Francey (1935, 1936) emphasized that the only "good" character to separate these two genera is the nature of the fruit, which in *Cestrum* is baccate and in *Sessea* a four-valved capsule. However, even this character, he adds, breaks down in *S. farinosa* (Urb. & Ekman) Francey, the young fruit of which is baccate, and in *C. strigillatum* Ruiz & Pavón and *C. lindenii* Dunal, in which the young fruit bears a cruciform suture at its apex, a feature typical of *Sessea*.

In that flowers and fruits tend to evolve as independent units (Davis & Heywood, 1963), it is not surprising to find both capsules and berries at different levels in an evolutionary scheme based primarily on floral morphology. Irrespective of their relative primitiveness, the occurrence of two types of fruits in the same subtribe or genus indicates differential evolutionary rates. The fruit has continued to change under varying conditions of climate, habitat, and selection for dispersal, and presumably different types of fruits may arise more than once, indicating a mosaic rather than a directional pattern of evolution. Constance (1955) summarized this phenomenon as follows: "analogous dehiscent or indehiscent, dry or fleshy, and one- or several-seeded fruit types can arise anywhere along this sequence, presumably as a result of selection pressure of biological demands." Detailed morphological studies of fruits in all three sections of *Brunfelsia* along with ecologically oriented field work will add much to our understanding of the dynamic relationships between these basic fruit types.

Specialized features are also found in the vegetative organs, which in many cases can be related directly to environmental conditions. Leaf size and texture are particularly variable according to existing climatic conditions. Species of humid tropical forests typically have relatively large leaves (*B. chiricaspi*, *B. hydrangeiformis*, *B. imatacana*, *B. pauciflora*, *B. plicata*). Those of the more exposed, drier habitats frequently exhibit smaller, often more coriaceous leaves (*B. brasiliensis*, *B. latifolia*, *B. nitida*, *B. obovata*, *B. rupestris*, *B. splendida*). There are many intermediate situations as well as species that show either type because they occur in both habitats (*B. uniflora*). Several of the Antillean species that inhabit serpentine soils have thick-coriaceous, linear leaves (*B. linearis* in Cuba, *B. densifolia* in Puerto Rico, Fig. 4). Other species that grow in high-altitude cloud forests have developed thick-coriaceous, very shiny leaves (*B. lactea* in Puerto Rico (Fig. 5), *B. dwyeri* in Panama, *B. uniflora* in Bolivia).

Another specialization in vegetative characters is the crowded or subverticillate arrangement of the leaves at the end of the stem (*B. hydrangeiformis*, *B. mire*). This generally appears in conjunction with a dense or capituliform inflorescence and very large leaves. The verticillate arrangement of the leaves in *B. rupestris* is of a slightly different nature, with crowded groups of leaves occurring at intervals along the stem.

An example of convergent evolution has apparently taken place in the leaves and fruits of *B. macrocarpa* and *B. chocoensis* of the Pacific lowlands of Colombia. These species belong to section *Franciscea* and section *Guianenses*, respectively. The leaves of these species are very similar in size, shape, and venation, and both species have fleshy, yellow fruits. However, the flowers indicate that they belong to different phyletic lines, although both are somewhat anomalous in their sections.

The digression of various species from the tropical forest environment and subsequent adaptation to more specialized ecological zones, such as rocky outcrops (*B. brasiliensis*), sandy shores (*B. latifolia*), marshes (*B. obovata*), *campo rupestre* habitat (*B. rupestris*), or coastal rocks (*B. americana*), are also indicative of evolutionary specialization. These aspects are discussed in "Ecology and Reproductive Biology." Further details are found in "Taxonomic Treatment" under individual species entries. The trends of specialization in the genus are summarized in Table 6.

IX. Geographical Distribution and Relationships[8]

The current distribution of species and subspecies, correlated with morphological, cytological,

[8] Plowman (1979) provides an in-depth discussion of the biogeography of *Brunfelsia*; the material in this section is intended as a summary only.—*Eds.*

TABLE 6. Trends in specialization of *Brunfelsia*.

Less specialized	More specialized
Plants of humid, tropical forests	Plants of other habitats
Leaves scattered on stem	Leaves crowded at branch tips or subverticillate
Leaves large, soft-leathery	Leaves small, coriaceous
Inflorescence terminal and subterminal	Inflorescence exclusively terminal or axillary
Inflorescence lax, branched	Inflorescence compact, sessile, and unbranched
Flowers few–many, small	Flowers solitary or few, large
Flowers scentless	Flowers fragrant
Calyx shorter than corolla tube	Calyx equaling corolla tube
Calyx terete, narrow	Calyx angled, inflated
Calyx present at base of fruit only	Calyx partially or totally enclosing fruit
Calyx not accrescent	Calyx more or less accrescent
Corolla tube straight, gradually dilated, and open at apex	Corolla tube curved and inflated at apex, then slightly constricted and thickened to form ring
Corolla lobes white or greenish, not changing color	Corolla changing color (white to yellow, purple to white)
Corolla lobes narrow, not overlapping, plane	Corolla lobes broad, overlapping, undulate to crenate
Fruits dehiscent	Fruits indehiscent
Capsule valves leathery or fleshy	Capsule valves thick, fleshy or bony, or thin-walled and dry

and other characters, provides us with the basis for erecting hypothetical phylogenies that indicate the possible historical relationships among present-day species. Unfortunately, no fossil remains of *Brunfelsia* or any related Solanaceae have been found to corroborate the relationships proposed here, nor have in-depth phylogenetic analyses been undertaken.

In *Brunfelsia* evidence from morphology and geographical distribution can be interpreted and evaluated against the background of the geological history and biogeographical patterns in other plants and in animals to infer the history of the genus. Such a scheme must be conjectural considering the paucity of data on several fronts, especially the all-important gaps in distributional patterns, the result of inadequate collecting. Nevertheless, the available data are full of implications that demand thoughtful consideration.

The major divisions of *Brunfelsia*, represented by three sections, appeared as the result of an early divergence in the ancestral, pre-*Brunfelsia* lineage, which in turn arose from primitive Salpiglossoid stock somewhere in South America. These three lines of divergence are evident today in the basic differences in floral morphology among the three groups and are associated with distinct and mostly allopatric areas of distribution. This suggests that the early differentiation of the ancestral pre-*Brunfelsia* was accompanied by geographical isolation in the three major areas in which they are found today.

The three sections of *Brunfelsia* are centered in three major areas: section *Brunfelsia* in the West Indies; section *Guianenses* in northern South America, primarily in the Amazon basin; and section *Franciscea* throughout most of tropical South America, excluding desert regions and the lowland forest of the Amazon.

All the species occurring in the West Indies belong to *Brunfelsia* sect. *Brunfelsia* (Fig. 9). This group, which exhibits both primitive and advanced characters, apparently diverged very early from a South American progenitor that was possibly similar to present-day section *Guianenses*. The most likely route of entry of the genus into the Antilles seems to be via the inner arc of the Lesser Antilles. These islands, which were formed in the late Cretaceous or early Tertiary period, have been volcanically active since the Eocene epoch to the present (Malfait & Dinkelman, 1972) [but see references cited in Liebherr, 1988, and Page & Lydeard, 1994, for competing theories for the origin of the Antilles—*Eds.*].

The hypothesis that the Lesser Antilles was the entry route of *Brunfelsia* into the Caribbean is based primarily on the present distribution of species. The group most closely related to the Antillean species is section *Guianenses*, which has its center of diversity in northern South America.

The only species of *Brunfelsia* that occurs today in the Lesser Antilles is *B. americana*, the least specialized and most widely distributed species of the genus. It is also found in Puerto Rico and the easternmost tip of Hispaniola. This plant has fleshy, bright orange fruits that may be carried

FIG. 9. Distribution of section *Brunfelsia*.

by birds from island to island. The agency of long-distance dispersal by birds cannot be ignored in considering the migration of *Brunfelsia* into the Caribbean, although a path of "island hopping" seems more logical. *Brunfelsia americana* occurs as far south in the Lesser Antilles as St. Lucia; currently prevailing arid conditions apparently exclude it from the southernmost islands of the chain. Although it is cultivated in St. Vincent and Trinidad, *B. americana* is not known to occur naturally in these islands at the present time.

No species are known from Central America north of Panama. This greatly detracts from the possibility that *Brunfelsia* may have entered the Antilles via some former land connection with Central America. Such a connection has been suggested with regard to the Nicaraguan Rise, a shallow area in the Caribbean extending from Nicaragua toward Jamaica [but see papers on Caribbean biogeography cited above—*Eds.*].

About 20 species of section *Brunfelsia* are known and are distributed throughout the major islands of the Caribbean, excluding the Bahamas, the eastern "limestone" islands, and the southernmost Lesser Antilles. There is a high degree of endemism on the largest islands, with about ten

FIG. 10. Distribution of sections *Guianenses* (dark gray shading) and *Franciscea* (pale gray shading); areas where both sections occur are shown in black.

endemic species in Cuba, six in Jamaica, one in Hispaniola, and three in Puerto Rico. Only *B. americana* is found on more than one island.

This radiation of species, typical of island evolution, appears to have arisen from reproductive and ecological isolation of populations. Many of the species are restricted to very local areas and appear to be effectively allopatric. Nothing is known of the breeding systems or pollinator–flower relationships that may have played a major role in reproductive isolation in these plants, especially among the sympatric species.[9] A particularly fertile area in this regard is the Oriente Province of Cuba, in which eight endemic species have been reported. These questions, however, are beyond the scope of the present study, in which only South American species and species complexes are treated in depth.

Brunfelsia sections *Guianenses* and *Franciscea* are essentially South American. Two species do extend into Panama but are clearly of South American origin. For the most part the two sections displace each other geographically (Fig. 10). Section *Guianenses*, with six species, occupies the lower Amazon basin, extending north into the Guianas, south to Bahía in Brazil, and west almost to the Colombian border. One species is isolated in the Chocó region of northeastern Colombia. Section *Franciscea*, which includes 15 species, is much more widespread, occurring over a large portion of the South American continent in a diversity of habitats. These species are found from the Caribbean coast south to about 30° latitude and from sea level to about 3300 m altitude.

[9] V. Fuentes, of the Botanic Garden, Havana, is presently working on this group; his results will be of great interest in resolving some of the questions posed here.—*Eds.*

Most species of section *Franciscea* are found in three major geographical provinces, corresponding to the "regional centers" recognized by Tryon (1972) for major areas of speciation in ferns. The most outstanding of these, in terms of numbers of species, is southeastern Brazil, which has 11 species of *Brunfelsia*, nine of which are endemic. The second major area is the Andean region, which has five species, three of which are endemic. The third region more or less agrees with the Guiana center of Tryon and includes parts of Guyana, Venezuela, and Roraima Territory in Brazil. Two species are found here; one is endemic, and the other is widely distributed.

The patterns of distribution of the species discussed here may reflect to some extent the amount of collecting in the different areas, especially where gaps in distributions are found in poorly collected areas such as the Amazon basin [see Nelson et al., 1990, for a discussion of this problem—*Eds.*] Recent intensive collecting sponsored by the New York Botanical Garden (New York, N.Y.) and the Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil) have added many new distribution records in formerly unknown areas. It is certain that the species that occur there will be shown to be more widely distributed as these areas become floristically better known.

It is here believed [see Plowman, 1979—*Eds.*] that most of the present distributions of *Brunfelsia* in the circum-Amazonian region, and probably in other parts of South America, are the result of climatic and geological changes that occurred during the Pleistocene epoch or more recently. Vuilleumier (1971), in a review article, summarized these events in view of their effects on the flora and fauna of the continent, with particular emphasis on the role of glaciation.[10]

Distribution patterns of *Brunfelsia* species occurring in the Andes correspond surprisingly well to the refugia of Haffer, Vanzolini, and Williams [see Plowman, 1979—*Eds.*]. It will be some time before these theories can be tested and retested by correlation with distribution patterns in other groups of organisms and with the ever-increasing body of knowledge of the geological and climatic history of the South American continent. But for the moment, the cyclic fragmentation and expansion of forests and their component species presents a working model for understanding the isolating barriers that have created the patterns of differentiation and geographical distribution in present-day species.

As here interpreted, the distribution and hypothetical relationships of *Brunfelsia* sect. *Franciscea* suggest a complex picture of speciation, migration, and extinction of populations. Some species are confined to relatively small areas in one of the three major centers of distribution. Others are found in more than one of these distant areas, either as the same species or as vicarious pairs. It is these plants that offer clues to the history of their origin and distribution over wide areas.

An outstanding aspect of the distribution in section *Franciscea* is the relationship between the Andean and southeastern Brazilian centers, which have one species and two pairs of vicarious species in common. In floral and fruit characters these species are relatively unspecialized with the exception of *B. hydrangeiformis*. In terms of the vegetative and inflorescence characters, *B. grandiflora* and *B. bonodora* are the least specialized and are considered to be relatively old species that may have given rise to others.

The present bicentric distribution of these species suggests that the two centers may have been in contact in the past. Several workers (Goodspeed, 1954; Smith, 1962; Vuilleumier, 1971) have offered the opinion that the intervening region (eastern Bolivia, Chaco, Mato Grosso) may have been wetter and cooler during the past, perhaps in conjunction with periods of glaciation or other climatic cycles. A more favorable climate would have permitted the development of tropical forests and an avenue for migration and gene exchange between the Andean region and southeastern Brazil.

Today this region is hot and dry and largely covered with *cerrado* vegetation, an arid formation of shrubs and stunted trees. It is an inhospitable habitat for wet tropical forest species, serving as an effective barrier to gene flow. The final uplift of the Andes was apparently responsible for the rain shadow now existing in the Chaco–Mato Grosso area. According to L. B. Smith (1962), the southward flow of heat from the Amazon and the northward encroachment of aridity from the south via the Chaco depression resulted in a climatic barrier that prevented further gene exchange between the two regions, creating many of the present-day disjunctions of species between them.

During the hypothetical period of more or less continuous forest between the Andes and southern Brazil, species were free to migrate in either di-

[10] The refugium hypothesis to which Plowman is alluding here and its present status are covered in a variety of works (e.g., Nelson et al., 1990; Mallet, 1993).—*Eds.*

rection. At this time the primitively Andean species migrated into the Brazilian highlands and to the Serra do Mar, where a secondary center of speciation developed.

There is evidence that some of these species eventually migrated back to the Andes during a period of forest expansion and were later severed from their parent populations by the unfavorable climate that ensued. This appears to have occurred in *B. uniflora*.

In many groups of plants, the area in which the greatest diversity of species occurs is also the area of origin of the group. This idea was particularly favored by Vavilov (1950), who worked with the wild progenitors of cultivated plants. Cain (1971), however, has pointed out that this by no means holds true for all groups of plants and has proposed the origin of secondary centers of speciation as follows:

> It is entirely possible, then, that a phyletic stock that has had its origin elsewhere, may, through migration, encounter a region in which there are numerous available ecological niches that are unsaturated, that is, in which competition pressure is low. Such a region may provide a variety of habitats with at least partial evolutionary radiation. It is apparent that such a region of polymorphism is not necessarily indicative of the original center of origin or of dispersal, but is a fortuitously derived center of differentiation. It may constitute a secondary center of evolution and of dispersal.

To summarize the hypothetical relationship in *Brunfelsia* sect. *Franciscea*, I suggest that this group first appeared in the Andean sector of South America and subsequently migrated to southeastern Brazil. Here the species encountered extremely favorable and diverse environments in which they became differentiated into several additional species. Secondary and perhaps repeated contacts with the Andean populations occurred as the newly evolved species migrated far and wide in periods of optimal climatic conditions. During unfavorable periods, large-scale extinction of populations occurred, creating the disjunct distributions that are seen today. Section *Guianenses* apparently originated in northern South America, probably in the Guiana–northeast Amazon region, and spread throughout the lower Amazon basin and to the Atlantic coast of Bahía. Other populations became isolated in the Chocó region, giving rise to the now disjunct *B. chocoensis*.

X. Taxonomic Treatment

Brunfelsia Linnaeus

Brunfelsia L., Sp. Pl.: 191. 1753, ("*Brunsfelsia*"); Gen. Pl. ed. 5:87. 1754, non *Braunfelsia* Par. 1894. Lectotype species designated by Knapp in Jarvis et al. (1993): *B. americana* L. Based on *B. flore albo, fructu croceo, molli*. Plumier, Pl. Am. 12. 1703; Nov. Pl. Am. Gen. t. 22. 1703.

Franciscea Pohl, Pl. Bras. Ic. 1: 1, t. 1–7. 1826. Lectotype species: *F. uniflora* Pohl. (See note under synonymy of section *Franciscea*.)

Brunfelsiopsis (Urb.) Kuntze in Post & Kuntze, Lex. 81. Dec. 1903 ("1904"). Type species: *Brunfelsia densifolia* Krug & Urb.

Evergreen shrubs or small trees, 0.3–10 m tall. **Branches** few to many, naked or leafy, terete. **Branchlets** terete or somewhat angled in cross section, glabrous or pubescent, the epidermis splitting lengthwise. **Leaves** alternate, with 5/13 phyllotaxy, scattered or subverticillate, simple, exstipulate, short petiolate, blade 3–30 cm long, 0.1–5 cm wide, elliptic, oblong, lanceolate, obovate to oblanceolate, rarely spathulate, ovate, linear or linear-oblong, apically acuminate, acute, blunt or rounded, entire at margin, basally narrowed, cuneate or blunt, glabrous to pilose on upper surface, glabrous to velutinous on lower surface, firmly membranaceous to thickly coriaceous, lateral nerves pinnate, 3–12, spreading, arcuately anastomosing near margin, veinlets finely reticulate. **Inflorescence** a cincinnal cyme or reduced to a single flower, terminal or axillary, subsessile, dense and compact, rarely lax and somewhat branched, with 1–many flowers. **Bracts** 1–3 per flower, 1–10 mm long, linear to lanceolate, caducous. **Flowers** white turning yellow, reddish purple, or violet-purple fading to pale violet or white, with or without fragrance. **Calyx** gamosepalous, 3–35 mm long, tubular to campanulate, glabrous or variously pubescent or glandular, light to dark green or purplish, membranaceous to subcoriaceous, 5-dentate, teeth 1–10 mm long, suberect, subequal, valvate in bud, triangular, ovate or lanceolate, apically acute, acuminate or truncate, minutely glandular-ciliolate; calyx in fruit persistent, enclosing capsule or present only at base, scarcely or rarely greatly accrescent, often becoming coriaceous and dotted with lenticels, striately nerved. **Corolla** gamopetalous, hypocrateriform, slightly zygomorphic with bilateral symmetry; tube 1.5–13 cm long, 1–5 mm in diameter, 1–24 times as long as calyx, cylindric, straight or

slightly curved, fleshy, gradually dilated or briefly inflated at apex, open at mouth or slightly constricted and thickened into fleshy white ring, glabrous or pubescent; limb 1.5–8 cm in diameter, 5-lobed, with quincuncial-imbricate estivation, perpendicular to tube or inclined at an angle, plane, undulate or crispate at margin; lobes subequal, obovate or broadly rounded, lateral margins overlapping or free, rarely abruptly deflexed. **Stamens** 4, didynamous, completely included within corolla tube or upper pair briefly exserted; filaments 2–10 mm long, inserted in uppermost part of corolla tube; lower pair posterior, shorter; upper pair anterior, longer, surpassing the pistil, slender, terete or somewhat flattened, curved posterially at apex; anthers 1–3 mm long, all fertile, rarely upper pair reduced or rudimentary, medifixed, simple, 1-celled, entire or slightly bilobate, oblong or orbicular-reniform, emarginate, dehiscing by a single longitudinal slit toward back of tube. **Ovary** superior, 1.5–3 mm long, sessile, subtended by short, nectariferous disc, bilocular, with 2 axile placentae; style filamentous, broader, and curved backward at apex, equaling the filaments; stigma 1–2 mm long, included between anthers, subentire, shallowly bilobate and subcapitate or briefly bifid in the form of a forceps with gaping lobes. **Ovules** numerous, anatropous. **Fruit** capsular or subbaccate, 1–5 cm long, subglobose to ovoid, bilocular or unilocular by dissepimental breakdown, valves entire, exocarp thin, membranaceous or subcoriaceous, smooth or becoming rugose-reticulate, with corky outgrowths, mesocarp thin coriaceous, dry at maturity, or thick, leathery or fleshy, endocarp thin, cartilaginous, drying brittle, sparingly dehiscent or indehiscent. **Seeds** few–numerous, 2–13 mm long, 1–7 mm in diameter, oblong, concave, angular, reticulate-pitted, reddish brown, partially immersed in fleshy placenta or drying free. **Embryo** straight or slightly curved, imbedded in endosperm; cotyledons flattened, ovate-elliptic. Chromosome number $2n = 22, 24$?

The genus *Brunfelsia*, as here circumscribed, consists of 46 species of tropical American shrubs or small trees. The genus is divided into three sections: *Brunfelsia*, *Guianenses*, and *Franciscea*. Section *Brunfelsia* consists of 22 species that are restricted to the West Indian islands. These species are not included in the present revision, but a brief description of the section and a list of the names of the species and synonyms are given in Appendix II. Section *Guianenses* contains six species that are found in South America, being particularly common in the Amazon basin and eastern Brazil. Section *Franciscea* consists of 18 species that are found in tropical areas of South America, two of which also occur in Central America.

Artificial Key to the Sections, Species, and Infraspecific Taxa of *Brunfelsia*

1. Corolla tube 6–24 times as long as calyx, white turning yellow with age, or reddish. West Indies ..... Section *Brunfelsia*
1. Corolla tube 1–4 times as long as calyx, purple fading to white or pale violet, or white to greenish white, not turning yellow. South and Central America
   2. Corolla tube open at mouth, not constricted; lobes narrow, deflexed at lateral margins or scarcely overlapping, white or greenish white ..... Section *Guianenses*
      3. Inflorescence sessile or with a very short peduncle; capsule dry at maturity, thin-walled
         4. Pedicels elongate, 13–20 mm long; calyx glabrous ..... 1. *B. amazonica*
         4. Pedicels short, 3–9 mm long; calyx teeth minutely glandular-papillose 4. *B. clandestina*
      3. Inflorescence pedunculate, the penducle occasionally very short but always visible; capsule at maturity fleshy (or unknown)
         5. Inflorescence bracts not ciliolate at margins, glabrous or very occasionally villous
            6. Leaves obovate to obovate-elliptic, with 4–5 lateral nerves; calyx 7–10 mm long. Brazil (Pará), Guianas ..... 5. *B. guianensis*
            6. Leaves ovate, with 5–9 lateral nerves; calyx 11–20 mm long. Brazil (Rio Tocantins) ..... 2. *B. burchellii*
         5. Inflorescence bracts ciliolate at the margins, otherwise glabrous
            7. Petiole 10–15 mm long; leaf blade 9–11 cm wide, with 6–7 lateral nerves; corolla limb 22–25 mm in diameter. NW Colombia, Panamá ..... 3. *B. chocoensis*
            7. Petiole 1–4 mm long; leaf blade 4–8 cm wide, with 8–12 lateral nerves; corolla limb 15–22 mm in diameter. E Guyana ..... 6. *B. martiana*

2. Corolla tube constricted at mouth forming thickened ring; lobes broadly rounded, overlapping at lateral margins, purple or violet fading to pale violet or white ..... Section *Franciscea*
    8. Calyx distinctly 5-angled, inflated, drying plicate
        9. Leaves cuneate to short acuminate at apex; pedicel and calyx glandular or villous pubescent; calyx teeth ovate to lanceolate, 2–7 mm long
            10. Leaves oblong-obovate to elliptic-lanceolate, the margins glabrous; calyx teeth ovate-lanceolate, 3–7 mm long. S Brazil ..... 12. *B. cuneifolia*
            10. Leaves obovate to elliptic-obovate, the margins villous ciliate; calyx teeth ovate, 2–4 mm long. Bolivia ..... 8. *B. boliviana*
        9. Leaves blunt to subacute at apex; calyx teeth broadly ovate, 1–4 mm long. E Brazil ..... 20. *B. obovata*
            11. Leaves firmly membranaceous to subcoriaceous; flowers (1)2–5; pedicels 1–8 mm long; calyx tubular, 16–22 mm long; corolla tube 1–1½ times as long as calyx ..... 20a. *B. obovata* var. *obovata*
            11. Leaves thick coriaceous; flowers (1–2)3–10; pedicels 5–12 mm long; calyx 10–16 mm long; corolla tube 1½–3 times as long as calyx ..... 20b. *B. obovata* var. *coriacea*
    8. Calyx terete, scarcely inflated, drying flat
        12. Leaves usually 16–31 cm long
            13. Flowers solitary on branch tips; calyx greatly accrescent in fruit; capsule fleshy, 4–5 cm in diameter. Pacific coast of Ecuador and Colombia ..... 18. *B. macrocarpa*
            13. Flowers 3 or more per inflorescence; calyx very slightly or not at all accrescent; capsule dry, thin-walled at maturity, less than 2 cm in diameter
                14. Corolla tube 1–1½ times as long as calyx; capsule completely enclosed in calyx; calyx 1.5–3.5 cm long. SE Brazil ... 15. *B. hydrangeiformis*
                15. Leaves subspathulate to broadly oblanceolate, reticulately rugose with sulcate nerves; pedicel 2–4 mm long; calyx 3–6 mm in diameter with yellowish brown pubescence; calyx teeth linear to linear-lanceolate, 4–10 mm long ..... 15a. *B. hydrangeiformis* subsp. *hydrangeiformis*
                15. Leaves oblong to oblong-lanceolate, smooth or sulcately nerved; pedicel 4–8 mm long; calyx 5–10 mm in diameter, glabrous or with sparse glandular trichomes; calyx teeth ovate to ovate-lanceolate, 2–4 mm long ..... 15b. *B. hydrangeiformis* subsp. *capitata*
            14. Corolla tube 2–5 times as long as calyx
                16. Corolla lobes deflexed at anthesis; flowers few, 4–7(20); leaves 7–12 cm wide. Amazonian Colombia and Ecuador ... 11. *B. chiricaspi*
                16. Corolla lobes spreading at anthesis; flowers (3)5–many; leaves less than 8 cm wide
                    17. Leaves subverticillate, with 8–13 lateral nerves; inflorescence dense, capituliform; corolla tube 25–38 mm long. Peru (Cuzco, Puno), Bolivia, W Brazil ..... 19. *B. mire*
                    17. Leaves scattered, with 5–9 lateral nerves; inflorescence lax, often short-branched; corolla tube 15–40 mm long. W South America ..... 14. *B. grandiflora*
                        18. Corolla tube 30–45 mm long; limb 35–52 mm across; capsule 1.7–2.2 cm long ..... 14a. *B. grandiflora* subsp. *grandiflora*
                        18. Corolla tube 15–30 mm long; limb 20–40 mm across; capsule 1–1.6 cm long 14b. *B. grandiflora* subsp. *schultesii*
        12. Leaves usually 2–15 cm long
            19. Calyx with short or long, nonglandular trichomes

20. Flowers 8–many per inflorescence; pedicels articulated with short, persistent peduncle; trichomes sparse to dense, yellowish to yellowish brown; corolla tube 17–22 mm long. SE Brazil .. 10a. *B. brasiliensis* subsp. *brasiliensis*
20. Flowers all 1–3 per inflorescence; pedicels not stalked; trichomes long, unbranched, pilose; corolla tube 25–32 mm long. S Brazil ..... 22. *B. pilosa*

19. Calyx glabrous or with sparse glandular hairs
21. Corolla tube 25–40 mm long
22. Flowers solitary on branch tips; leaves thick coriaceous; capsule rugulose, pericarp leathery, 1–4 mm thick. Panamá .. 13. *B. dwyeri*
22. Flowers 1–many per inflorescence; leaves membranaceous to subcoriaceous; capsule smooth, pericarp thin-walled, drying brittle
23. Corolla tube 1–2 times as long as calyx; capsule completely enclosed by calyx
24. Pedicel articulating with short peduncle; peduncle 2–5 mm long; corolla limb 25–32 mm across; leaves 1.2–2.2 cm wide. SE Brazil .. 10b. *B. brasiliensis* subsp. *macrocalyx*
24. Pedicels sessile or nearly so; corolla limb 40–80 mm across; leaves 2–6.5 cm wide
25. Leaves oblong to oblong-lanceolate, with 5–11 lateral nerves; flowers 1–11; pedicel 11–25 mm long; corolla tube 1–1½ times as long as calyx. SE Brazil .. 21. *B. pauciflora*
25. Leaves oblong-elliptic to oblong-obovate, with 6–7 lateral nerves; flowers 1–2; pedicel 8–9 mm long; corolla tube 1½–2 times as long as calyx. E Venezuela ..... 16. *B. imatacana*
23. Corolla tube 2–5 times as long as calyx; capsule exceeding the calyx in fruit
26. Flowers 1–3(4) per inflorescence; leaves elliptic-obovate, apically blunt to acute. S Brazil, Paraguay, Argentina .... 7. *B. australis*
26. Flowers (3)5–many per inflorescence; leaves oblong-lanceolate to lanceolate, apically acuminate. W South America ..... 14. *B. grandiflora*
21. Corolla tube 15–25 mm long
27. Flowers all solitary. Widespread ..... 24. *B. uniflora*
27. Flowers >1 per inflorescence
28. Leaves congested near branch tips, with strongly revolute margins, 1–4 cm long. *Campo rupestre*, Brazil .. 23. *B. rupestris*
28. Leaves scattered along branches, not strongly revolute, usually >5 cm long. Forests
29. Leaves elliptic-oblong, ovate or obovate, blunt or abruptly short acuminate. Rio de Janeiro ..... 17. *B. latifolia*
29. Leaves narrow-elliptic to oblong-lanceolate, apically acuminate
30. Pedicels 6–12 mm long; calyx in fruit nearly as long as capsule. SE Brazil ..... 9. *B. bonodora*
30. Pedicels 2–6 mm long; calyx in fruit half as long as capsule or less. W South America .. 14b. *B. grandiflora* subsp. *schultesii*

Brunfelsia* sect. *Guianenses Plowman in Hawkes, J. Linn. Soc. (Bot.) 76: 294. 1978.

TYPE SPECIES—*Brunfelsia guianensis* Benth. in DC., Prodr., 10: 200. 1846.

Shrubs to 2 m tall. Inflorescence terminal and axillary. Flowers small, 1–7 per inflorescence. Corolla white or greenish white, tube 2–3 times as long as calyx, open at mouth, not constricted, the lobes narrow, usually with deflexed margins. Stigma briefly bifid, in the form of a forceps. Capsule dry or fleshy at maturity. South America.

1. *Brunfelsia amazonica* C.V. Morton, Proc. Biol. Soc. Wash. 62: 151. 1949. Type: BRAZIL Amazonas: Manaus, Estrada do Raiz, silva secundaria, non inundabilis, *manacá*, 24 Mar. 1937, *Ducke 430* (holotype, US 1693434; isotypes, A, F-902265, K, MO-1156896, NY, R-75434, S). **Figure 11.**

Shrub or small tree 1.5–2.5 m tall. **Branches** spreading, knobby. **Bark** buff to reddish brown, cracked in longitudinal fissures. **Branchlets** shiny, glabrous, light, yellowish brown. **Leaves** scattered on branchlets, blade 6.5–12 cm long, 2.5–5 cm wide, elliptic-oblong to lanceolate, abruptly acuminate, acumen often oblique, broadly cuneate to narrowed at base, glabrous, dark green above, pale green beneath, firmly membranaceous, lateral nerves 5–8(10), straight; petiole 2–5(8) mm long, transversely corrugate with cracked epidermis, glabrous. **Inflorescence** terminal or axillary, sessile with 1–2(5–6) flowers. **Flowers** white or greenish white, fragrant. **Bracts** 1–2 per flower, 2–6 mm long, linear to lanceolate, glabrous, caducous. **Pedicel** curved in bud, becoming erect, 13–20 mm long, 1 mm in diameter, slender, thickened toward apex, glabrous. **Calyx** 8–12 mm long, 5–8 mm in diameter, tubular-campanulate, slightly inflated, obovate in bud, glabrous, green, membranaceous, teeth 2–6 mm long, erect, somewhat unequal, ovate-lanceolate, apically blunt to acuminate; calyx in fruit, enclosing capsule at base. **Corolla** tube 20–25 mm long, 1.5–3.0 mm in diameter, twice as long as calyx, cylindric, slightly dilated toward mouth, glabrous, minutely glandular at mouth; limb 15–25 mm in diameter, spreading, lobes 6–11 mm long, subequal or the posterior lobe somewhat larger, oblong to obovate, somewhat convex, blunt or rounded at apex, the sides of the lobes reflexed after anthesis, narrowed slightly toward base. **Stamens** inserted at middle of tube, included; filaments subligulate, upper pair 5 mm long, lower pair 2–3 mm long; anthers 1–1.5 mm in diameter, orbicular-reniform. **Ovary** 1.5 mm long, 1 mm in diameter, narrowly conical; style 16–18 mm long; stigma 1 mm long, bifid, upper lobe somewhat larger. **Fruit** 10 mm in diameter, globose, apiculate at apex, green, smooth, pericarp thin, about 0.2 mm thick, dry at maturity, sparingly dehiscent. **Seeds** 8–10, 5–6 mm long, 3 mm in diameter, oblong-reniform, flattened on 1 or 2 sides, angular, dark brown, reticulate-pitted with a medial hilum. **Embryo** 3 mm long, slightly curved; cotyledons about 0.5 mm long, elliptic.

DISTRIBUTION—Brazil (Amazonas). See Figure 15.

SPECIMENS EXAMINED—**BRAZIL. Amazonas:** Manaus, Estrada da Raiz, 18 Mar. 1943, *Ducke 430* (paratype, MG, US); perto da Estrada da Raiz, 22 Mar. 1932, *Ducke sp. nov.* (GH, RB); Mata do Aleixo, 4 Mar. 1945, *Fróes 20535* (NY, US); Uypiranga, Rio Negro, perto de Manaus, 21 Feb. 1923, *J.G. Kuhlmann 943* (GH, RB); road Manaus (Cacau-Pireira) to Manacapuru, km 25, 3 Jan. 1967, *Prance, Pena & Ramos 3880* (F, INPA, K, MG, P, R, S, US); ad oram meridionalem Rio Negro, usque ad concursum flum. Solimões, May 1851, *Spruce 1495* (BM, BR, CGE, F, G, GH, K, LE, MG, NY, P, RB, W); *Rio Negro, Tapuruquara, Santa Izabel, *Black 48-2905* (IAN).

This species was first collected by Spruce in the middle of the last century and distributed under the name *B. spruceana* to the world's herbaria. This name was recorded but not validly published by Schmidt, who placed it in synonymy with *B. maritima* Benth.

Brunfelsia amazonica is a very local species, known only from the environs of Manaus at the mouth of the Rio Negro in Brazil. Notwithstanding the intensity of collecting in this region, *B. amazonica* has not been collected often. It is a very distinct species of section *Guianenses* and is easily separated from *B. guianensis* and *B. chocoensis* by the longer pedicels, the oblong-lanceolate leaves, and dry, thin-walled fruit, and from *B. martiana* by the longer pedicels and smaller leaves.

Brunfelsia amazonica grows in open secondary forests on the southern bank of the Rio Negro in white sandy soil. It is known to flower from January to May; fruits have been collected only in

FIG. 11. *Brunfelsia amazonica.*

May. Like many brunfelsias in Brazil, this species is locally called *manacá.*

2. ***Brunfelsia burchellii*** Plowman, Fieldiana Bot. n. s. 8: 9. 1981. Type: BRAZIL. Goiás: Porto Real (now Porto Nacional), ford of Igarapé, 1828–1830, *Burchell 8527* (holotype, P; isotypes, K, L).[11] **Figure 12.**

Shrub. Mature **branchlets** 2–3 mm in diameter, spreading, with shiny, yellowish to dark brownish, longitudinally cracked bark. **Leaves** scattered along stem, short petiolate, blade 70–180 mm long, 30–75 mm wide, broadly to narrowly ovate, apically acuminate with a long, pointed, often falcate acumen, sometimes abruptly acuminate, minutely ciliolate at margin, basally rounded to obtuse, glabrous on both sides, dull or somewhat shiny, medium green above, dull, paler green beneath, firmly membranaceous to chartaceous, the lateral nerves 5–9, strongly arcuate, anastomosing near margin, nerves prominent on lower surface; petiole 1–6 mm long, with a few scattered glandular hairs, glabrescent. **Inflorescence** terminal on current year's branchlets, very briefly pedunculate, with 1–3 flowers. **Peduncle** 14 mm long, persistent, sparsely glandular-pubescent, glabrescent. **Bracts** 1–3 per flower, 4–20 mm long, linear to lanceolate, apically acuminate, glabrous or villous at nerves and margin, caducous. **Flower** color unknown. **Pedicel** 4–8 mm long, 1 mm in diameter, sparsely glandular-pubescent, glabrescent. **Calyx** 11–20 mm long, 5–9 mm in diameter, tubular or tubular-campanulate, terete, with scattered glandular hairs, glabrescent, striately nerved, teeth 2–6 mm long, unequal, triangular-ovate, apically acute to acuminate, minutely gland-tipped. **Corolla** tube 24–28 mm long, 1.5–2 mm in diameter, 1½–2 times as long as calyx, straight, glabrous or bearing few scattered glandular hairs, orifice 5 mm in diameter; limb 18–30 mm in diameter, spreading, lobes subequal, rounded, overlapping at the lateral margins. **Stamens** inserted in upper part of corolla tube; filaments 1 mm wide, straplike, the anterior pair 3.5–6 mm long, apically slightly incurved or suberect, the posterior pair 3–4 mm long; anthers 1 mm in diameter, orbicular-reniform. **Ovary** 1.5 mm long, conical-ovoid; style 20–21 mm long, broadened and incurved at apex; stigma included between pairs of anthers, 1 mm long, briefly bifid, upper lobe slightly larger. **Fruit** and **seed** unknown.

DISTRIBUTION—Basin of the upper Rio Tocantins (Goiás State) and adjacent Maranhão State, Brazil. See Figure 15.

SPECIMENS EXAMINED—**BRAZIL. Goiás:** Porto Real, Porto Real to Igarapé, 1828–1830, *Burchell 8415* (L); about village, *Burchell 8494* (K); at entrance to village, *Burchell 8653* (K); "about the Manga" (cf., Rio dos Mangues, where it meets the Tocantins), *Burchell 8752* (CH). **Maranhão:** Island of São Luiz, Estrada do Barreto, Feb.–Mar. 1939, *Fróes 11620* (A, F, NY, S, US).

Brunfelsia burchellii is known from only a few collections by William J. Burchell in the vicinity of Porto Real (now called Porto Nacional) on the upper Rio Tocantins 150 years ago. Unfortunately, these specimens bear no field data, and the plant has not been recollected in this region. A modern collection by Fróes from São Luiz Island, more than 1,000 km north of Porto Nacional, is tentatively assigned to *B. burchellii* but lacks mature flowers or fruits and differs somewhat in leaf venation.

Brunfelsia burchellii appears to be most closely related to *B. guianensis*, from which it differs by the ovate, acuminate leaves, the longer tubular calyx, and the broadly rounded corolla lobes. With *B. guianensis*, *B. burchellii* is provisionally placed in section *Guianenses* on the basis of the gradually dilated and not apically constricted corolla tube.

Two additional collections with ovate acuminate leaves appear to be related to *B. burchellii* but cannot be placed with certainty. One of these, *Ducke s.n.* (RB 18141), was collected at Bragança in Pará and bears small, white, terminal, solitary flowers and immature leaves. The other, *Sucre & da Silva 9204* (F, RB), was collected at Buriti dos Lopes, Piauí, and has rather shiny, thick leaves and immature fruits completely enclosed in persistent, accrescent calyces.

3. ***Brunfelsia chocoensis*** Plowman, Bot. Mus. Leafl. 23(6): 245, t. 14. 1973. Type: COLOMBIA. Antioquia: Chigorodo, forest just southeast of Chigorodo, 45 km S of Turbo, alt. 50 m. Shrub 2 m high. Flowers rather conspicuous, of a peculiar flat white color, like unglazed paper, 15 Apr. 1945, *Haught 4563* (holotype, UC M 048365; isotypes, NY, COL 109727). **Figure 13.**

[11] All Burchell localities are taken from his itinerary, published by Smith and Smith (1967).

FIG. 12. *Brunfelsia burchellii*. Reproduced courtesy of the Field Museum of Natural History.

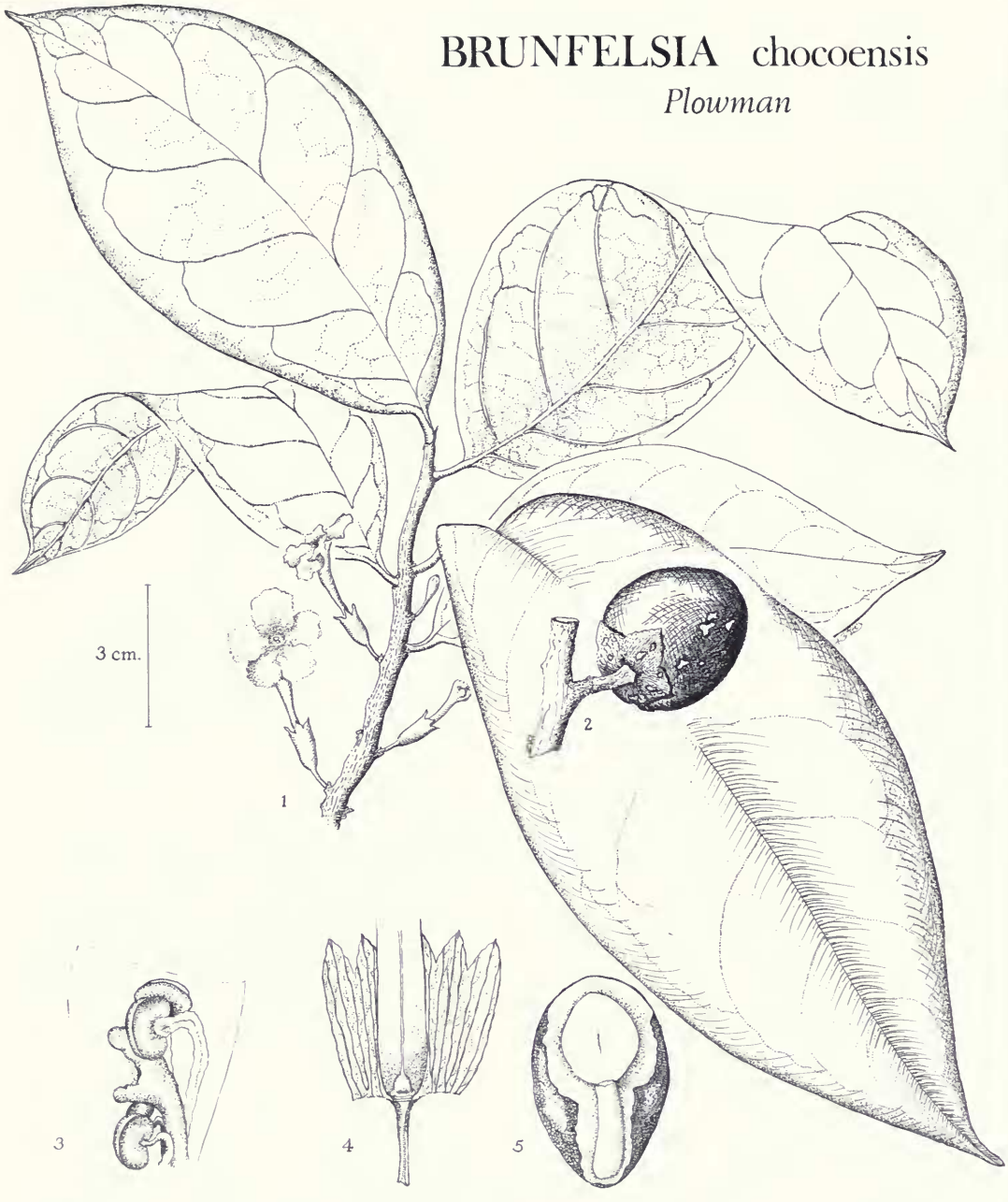


FIG. 13. *Brunfelsia chocoensis*. Reproduced courtesy of the Botanical Museum of Harvard University.

Shrub 2 m tall. **Branches** sparse, terete, somewhat knobby at nodes, naked, gray or grayish brown. **Branchlets** 3 mm in diameter, glabrous, shiny, light grayish brown. **Leaves** few, usually crowded at ends of branchlets, blade 18–28 cm long, 9–11 cm wide, elliptic to oblong, abruptly to long acuminate at apex, acumen often subfalcate, obtuse at base, glabrous, dull, dark green above, pale green beneath, firmly membranaceous, lateral nerves 6–7, spreading; petiole 10–

15 mm long, stout, brown. **Inflorescence** subsessile, terminal, 1-flowered, or, on previous branches, axillary with 1–3 flowers. **Flowers** white, fragrant. **Bracts** 2–4 mm long, ovate to ovate-lanceolate, concave, ciliolate at margin, caducous. **Pedicel** 5–6 mm long, erect, slender, glabrous. **Calyx** 8–12 mm long, 3–6 mm in diameter, tubular-campanulate, globose in bud, glabrous, firmly membranaceous, veinlets prominulous, reticulate, teeth 2–4 mm long, erect, ovate, blunt to acute; calyx in fruit to 13 mm long, persistent, dotted with lenticels. **Corolla** tube 22–27 mm long, 2–2.5 mm in diameter, twice as long as calyx, gradually dilated toward mouth, glabrous; limb 22–25 mm in diameter, spreading from rounded mouth 5 mm in diameter, the lobes 8–10 mm long, subequal, rounded at apex, rarely emarginate, slightly overlapping at margin above base. **Stamens** included in upper third of tube; filaments 5 mm long, somewhat flattened, lower pair curved at apex, upper pair suberect, glabrous; anthers 2 mm long, orbicular-reniform, light brown. **Ovary** 2.5 mm long, ovoid; style 10–20 mm long, slender; stigma 1.5 mm long, bifid, gaping, the upper lobe somewhat larger. **Fruit** 2–3 cm long, 2–3 cm in diameter, globose to ovoid, smooth, yellow when ripe, mesocarp soft, fleshy, up to 1.5 mm thick, endocarp thin, cartilaginous. **Seeds** few, 2–5, 8–10 mm long, 6–7 mm in diameter, ovoid-ellipsoid, angular, dark brown, reticulate-pitted. **Embryo** 8 mm long, straight; cotyledons 3.5 mm long, widely elliptic.

DISTRIBUTION—Panamá, Colombia. See Figure 15.

SPECIMENS EXAMINED—**PANAMÁ. Darién:** Cerro Pirre, 11 Apr. 1967, *Bristan 566* (ECON, OSU), *Bristan 569* (ECON, OSU), **Bristan 1220* (MO), **Duke 5300* (MO), **Gentry & Clewell 7138* (MO); *along Río Armila, WSW of Puerto Obaldía, *Mori 6828* (MO). **COLOMBIA. Chocó:** Hydro Camp No. 14, Río Salaquí, 6 days upstream from Río Sucio, alt. ca. 200 m, 23 May 1967, *Duke 11351* (ECON); *hills below first rapids on Río Truando, *Duke 13331* (MO).

Brunfelsia chocoensis is restricted to the northernmost part of the Chocó region of Colombia in the low-lying basin of the Río Atrato, an area bound by the Serranía de Baudo in the west and the Serranía de Abibe in the east. Its range extends northward to Cerro Pirre across the Panamanian border. Although additional collecting may reveal a larger area for the species, *B. chocoensis* appears to be endemic at this low elevation (50–200 m) in swampy forest. In 1945 it was reported as a common species at Chigorodo, the type locality. I failed to find the plant on a collecting trip there, primarily because of the large-scale destruction of the forests for agriculture and pasturage.

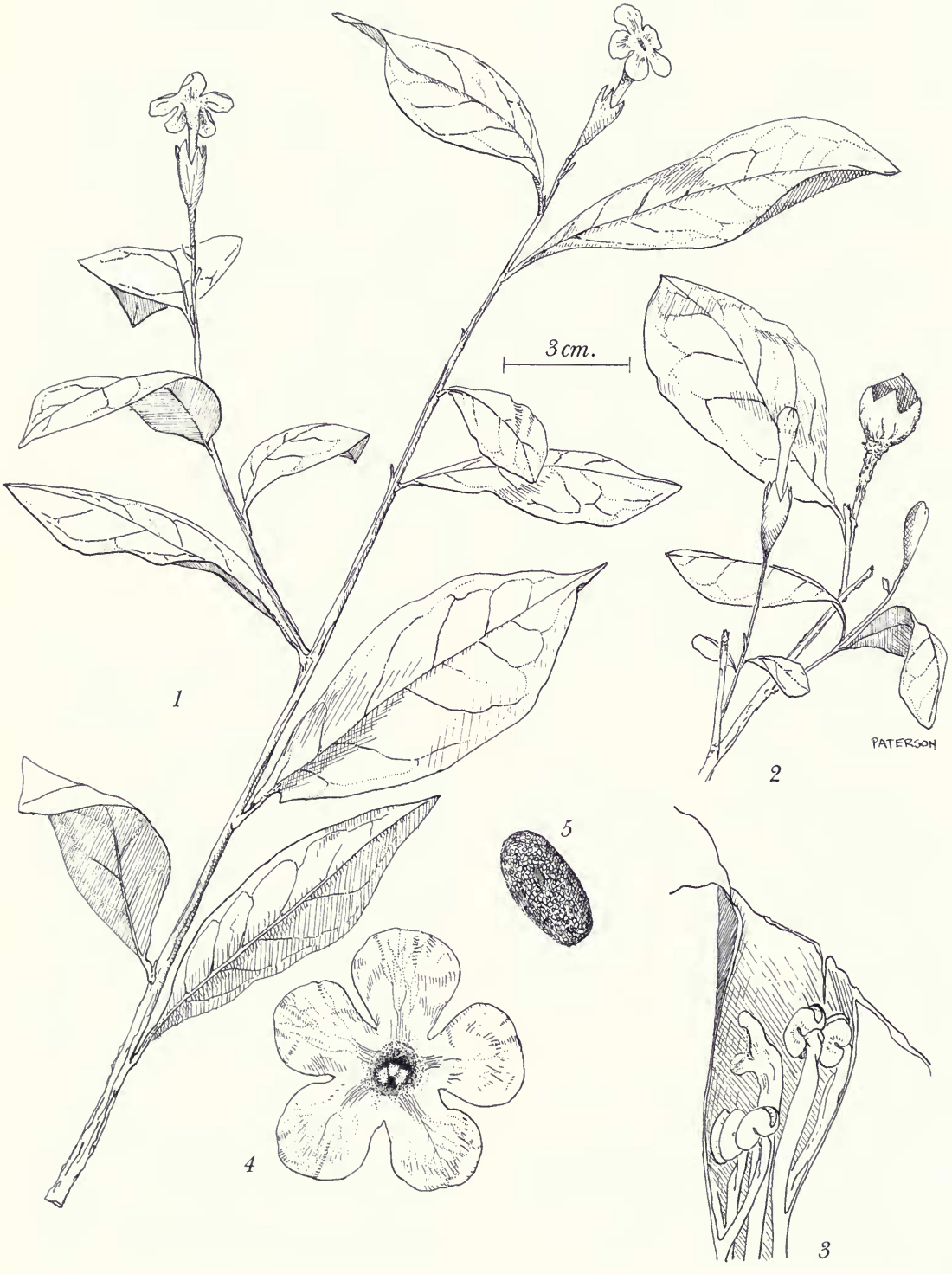
Most closely related to *B. guianensis* of the Guianas and northern Brazil, this species differs in having much larger leaves with longer petioles, longer pedicels, and broader corolla lobes. The fruit of *B. chocoensis* is very similar to the fleshy capsules of both *B. guianensis* and *B. macrocarpa*. Although *B. chocoensis* was originally thought to be related to *B. macrocarpa*, it now seems that the resemblance is only superficial. The flowers of *B. macrocarpa* are very large and purple, fading to white with age in the manner of species of section *Franciscea*. In addition, the calyx of *B. macrocarpa* is accrescent and encloses the mature fruit, whereas the calyx in *B. chocoensis* is small and present only at the base of the fruit.

Data from herbarium labels (*Bristan 566* and *569*) indicate that the fleshy, yellow fruits of this species are edible and that the flowers are fragrant.

4. *Brunfelsia clandestina* Plowman, Fieldiana Bot. n.s. 8: 11. 1981. Type: BRAZIL. Bahía: Município Itapebí, Fazenda Lombardia, BR 101 ao lado leste. Arbusto de 3 m de altura. Flor branca. Capoeira, 12 Aug. 1971, *T. S. dos Santos 1777* (holotype, CEPEC 7086; isotype, F 1849031). **Figure 14.**

Shrub or treelet to 6 m tall. **Trunk** to 8 cm in diameter. **Bark** on trunk and branches yellowish brown, cracking longitudinally and transversely, shedding in thin, irregular flakes. **Branchlets** 1.5–2 mm in diameter, glabrous, grayish to dark, reddish brown, more or less shiny, cracked longitudinally. **Leaves** short petiolate, the blade 35–120 mm long, 15–50 mm wide, elliptic to oblong-lanceolate, rarely lanceolate or obovate, apically acute to acuminate, the apex itself obtuse, basally acute or obtuse, glabrous or rarely sparsely puberulent on the costa beneath, medium green above, somewhat lighter green beneath, shiny on both surfaces, chartaceous to subcoriaceous, rarely coriaceous, the lateral nerves 6–8, mostly straight, forming an angle of 45–70° with midrib, anastomosing with the arcuate marginal nerve 3–6 mm from margin; petiole 26 mm long, glabrous

BRUNFELSIA clandestina *Plowman*



or with scattered glandular hairs. **Inflorescence** terminal or subterminal on mature or newly formed twigs of current season, with or without a short peduncle, 1- or 2-flowered. **Bracts** 0–3, 2–6 mm long, linear or cymbiform, truncate at apex, sparsely pubescent or glandular-pubescent, caducous. **Flowers** white. **Pedicel** 3–9 mm long, 1 mm in diameter, glabrous, becoming thicker in fruit, to 3 mm in diameter, warty-lenticellate. **Calyx** 8–16 mm long, 3–7 mm in diameter, tubular or tubular-campanulate, terete, glabrous, light green, membranaceous, teeth 2–5 mm long, subequal, triangular-ovate, apically acute or acuminate, the apex itself blunt and minutely glandular-papillose; calyx in fruit persistent, 11–16 mm long, shiny, coriaceous, striately nerved, tightly enclosing basal half of capsule. **Corolla** 18–25 mm long, 1–3 mm in diameter, tube 1.5–2 times as long as calyx, straight, glabrous, rarely with a few glandular hairs, orifice 3–5 mm across; limb 15–26 mm in diameter, spreading, inclined, lobes 6–10 mm long, subequal, expanding somewhat with age, broadly obovate to rounded. **Stamens** inserted in upper part of corolla tube; filaments 0.6–1 mm wide, strap-shaped, the anterior pair 3–5 mm long, incurved at apex, included, the posterior pair 1.5–3 mm long; anthers 1 mm in diameter, orbicular-reniform. **Ovary** 1–1.5 mm long, 0.8–1.2 mm in diameter, conical-ovoid, with about 10–12 ovules per locule; style 16–20 mm long, incurved at apex; stigma 1–1.5 mm long, briefly bifid, upper lobe slightly larger. **Capsule** dry at maturity, 13–20 mm long, 13–15 mm in diameter, ovoid to subglobose, apiculate, smooth, shiny, dark green at maturity; pericarp thin, 0.5–1 mm thick, crustaceous. **Seeds** ca 9–15, 5–7 mm long, 2.5–3 mm in diameter, oblong-reniform, terete, or somewhat flattened on one side, dark brown, reticulate-pitted. **Embryo** 3–6 mm long, straight; cotyledons 1–2 mm long, ovate to elliptic, radicle 2–4 mm long.

DISTRIBUTION—States of Bahía and Espirito Santo, Brazil. See Figure 15.

SPECIMENS EXAMINED—**BRAZIL. Bahía:** "Prov. Jacobina," 1841, *Blanchet 3354* (G, LE, W), 1843, *Blanchet s.n.* (C, G, W); "Igreja Velha," 1841, *Blanchet 3352* (BM, BR, G, P); Serra de Sincorá, Brejão a Iracema, 17 Feb. 1943, *Fróes 20210* (IAN, NY, US); Município Jaguaquara, Jaguaquara a Apuerama, 4 Oct. 1972, *Pinheiro 1980* (CEPEC, F, NY); Município Itacaré, Itacaré–Ubaitaba, 14 Apr. 1980, *T.S. dos Santos 689* (CEPEC, F); Rodovia BA 654, km 6 ao oeste de Itacaré, approx. 14°18′S, 39°02′W, ca. 60 m, 12 Apr. 1980, *Plowman, Mattos Silva & dos Santos 10066* (CEPEC, F), *Plowman, Mattos Silva & dos Santos 10087* (CEPEC, F); Município Itambé, Itambé, 24 Nov. 1942, *Fróes 20067* (IAN, NY); Município Itajã do Colônia, 12 km da estrada em direção a Feirinha ao lado oeste, margem esquerda do Rio Corró, 23 Oct. 1969, *T.S. dos Santos 433* (CEPEC, F); Município Belmonte, Estação Experimental Gregório Bondar, km 58 da rodovia Belmonte/Itapebi, 16 May 1979, *Mattos Silva et al. 357* (CEPEC); Município Santa Cruz de Cabrália, Reserva Biológica do Pau-Brasil, 18 Sep. 1971, *T.S. dos Santos 1964* (CEPEC, F); cerca de 16 km a oeste de Porto Seguro, 21 Mar. 1978, *Mori et al. 9775* (CEPEC, F); antiga rodovia que liga a Estação Ecológica de Pau-Brasil a Santa Cruz, 5–7 km ao NE da Estação, ca. 12 km ao NW de Porto Seguro, 16°23′S, 39°8′W, ca 80–100 m, 5 Jul. 1979, *Mori et al. 12082* (CEPEC, F, US); Município Guaratinga, rodovia Guaratinga/São Paulinho, km 25, 2 Apr. 1973, *Pinheiro 2086* (CEPEC, F); without locality, 1857, *Blanchet s.n.* (G, L, LE); without locality or date, *Blanchet 1455* (F), *Blanchet s.n.* (F, MG, NY); *Município de Cairu; Estrada Cairu–Itabera, 8 km S of Cairu, *Carvalho & Gatti 795* (F). **Espirito Santo:** Linhares, Vale do Rio Doce, km 6 da rodovia BR 101, lado sul, 30 Sep. 1971, *T.S. dos Santos 2015* (CEPEC, F, NY).

Brunfelsia clandestina was first collected by the Swiss collector Blanchet in the state of Bahía more than 100 years ago. Following earlier authors, I originally assigned Blanchet's several collections of the species to *B. uniflora*, although I pointed out certain differences between typical *B. uniflora* and the Blanchet material (Plowman, 1973). These early collections lacked adequate field data and fruiting material [see Plowman, 1981—*Eds.*].

Brunfelsia clandestina superficially resembles several other brunfelsias and may be confused with them. Complete specimens, including field data and flower color, are essential for making positive identifications. *Brunfelsia clandestina* appears to be most closely related to *B. martiana*, a

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FIG. 14. *Brunfelsia clandestina*. Reproduced courtesy of the Field Museum of Natural History.

FIG. 15. Distribution of species in section *Guianenses*: *Brunfelsia amazonica* (open square), *B. burchellii* (open triangle), *B. chocoensis* (open circle), *B. clandestina* (solid triangle), *B. guianensis* (solid square), and *B. martiana* (solid circle).

species that also grows in the moist forests of Bahía. *Brunfelsia clandestina* differs in having much smaller leaves with fewer lateral nerves and one- or two-flowered inflorescences that are borne terminally. In dried specimens, *B. clandestina* may also be confused with *B. uniflora*, a species known from Bahía but belonging to a different section of the genus (section *Franciscea*). *Brunfelsia clandestina* differs mainly in having dark brown or reddish brown branchlets, glabrous or nearly glabrous leaves and twigs, and a tubular-campanulate rather than narrowly tubular calyx. The flowers of *B. clandestina* are white; those of *B. uniflora* are violet, fading to white with age.

Brunfelsia clandestina grows in the moist coastal forests of southern Bahía and Espirito Santo. Earlier collectors in Bahía also found this species further inland in areas formerly covered with mesophytic forest. Most of these areas have now been converted to pastures (Mori & Mattos Silva, 1979). The last collection in the drier, interior part of Bahía was made in 1943.

5. ***Brunfelsia guianensis*** Benth. in DC., Prodr., 10:200. 1846. Lectotype (designated here): SURINAM. Without locality or date, *Hostmann 1278* (lectotype, K; isolectotypes, G, S, W). Lectoparatype: FRENCH GUIANA. Cayenne, 1820, *Perrottet s.n.* (G, G-DC, non vidi; photograph, NY). **Figure 16.**

Shrub to treelet 1–3 m tall. **Branches** lax, spreading. **Branchlets** terete, becoming knobby at nodes, glabrous, rarely pubescent, epidermis split-

FIG. 16. *Brunfelsia guianensis*. Reproduced courtesy of the Linnean Society, London. (First published in Plowman, 1978: *Botanical Journal of the Linnean Society,* **76:** 294–295.)

ting in longitudinal cracks, eventually shedding in flakes, light to dark brown. **Leaves** with blade 6–15 cm long, 2–6.5 cm wide, obovate to elliptic, rarely lanceolate, abruptly acuminate at apex, acumen often subfalcate, cuneate to narrowed at base, glabrous, dull, dark green above, paler green beneath, firmly membranaceous, lateral nerves 4–5, arcuate; petiole 3–8 mm long, slender, glabrous, rarely pubescent. **Inflorescence** axillary or terminal, with 1–2 flowers. **Flowers** white, odorless.

Bracts 1–2 per flower, 2–10 mm long, linear-lanceolate or squamiform, glabrous, caducous. **Pedicel** 2–5 mm long, slender, short, glabrous. **Calyx** 7–10 mm long, 4–7 mm in diameter, ovoid-campanulate, inflated, rarely tubular-campanulate, ovoid in bud, glabrous, green, membranaceous, sparsely veined, teeth usually unequal, two posterior teeth somewhat shorter, 2–5 mm long, ovate, acute to acuminate at apex; calyx in fruit persistent, becoming somewhat coriaceous, splitting on 1 or more sides. **Corolla** tube 20–26 mm long, 1–1.5 mm in diameter, 2.5–3 times as long as calyx, slender, straight or curved, gradually dilated above middle, glabrous, greenish white to white, limb 15–22 mm in diameter, spreading, lobes 6–8 mm long, subequal, oblong-obovate to spathulate, narrowed at base, rounded or blunt at apex, lateral margins strongly reflexed, white, occasionally with traces of purple. **Stamens** included within tube; filaments slender, suberect, ligulate, anterior pair 4–5 mm long, posterior pair 2–4 mm long; anthers 1 mm in diameter, orbicular-reniform. **Ovary** 1.5–2 mm long, 1 mm in diameter; ovoid-conical, style slender, broadened toward apex; stigma included between anthers, briefly bifid, upper lobe slightly larger. **Fruit** 2.5–3.2 cm in diameter, 2.5–4 cm long, globose to ovoid, smooth, yellow when ripe, exocarp thin, rubbery, mesocarp soft, fleshy, 5–8 mm thick, endocarp thin, cartilaginous. **Seeds** 7–10, 10–13 mm long, 5–7 mm in diameter, oblong, flattened on 1 or 2 sides, angular, reddish brown to nearly black, reticulate-pitted. **Embryo** 8 mm long, straight; cotyledons 2 mm long, elliptic.

DISTRIBUTION—Surinam, French Guiana, Brazil. See Figure 15.

SPECIMENS EXAMINED—**SURINAM.** In montibus Nassau, in forest near km 0.1, 17 Feb. 1949, *Lanjouw & Lindeman 2137* (K, NY); near km 6, 7, 10 Mar. 1949, *Lanjouw & Lindeman 2564* (K, NY); along creek with large rapids, 24 Mar. 1949, *Lanjouw & Lindeman 2888* (K, NY); Saramacca River, Jacob Kondre, 19 Jun. 1944, *Maguire 23894* (NY); Jodensavanne-Mapane creek area; Dist. Brokopondo, N of Brokopondo, 55°W, 5°N, 14 Feb. 1966, *van Donselaar 3114* (NY); ad flum. Paloemeu et Tapanahoni confl., 3°20′N, 55°27′W, 10 Apr. 1963, *Wessels Boer 1195* (NY, US); without locality, Sep. 1853, *Wüllschlagel 1505* (W); *Brownsberg Nature Park; 90 km S of Paramaribo, Mori, *Bolten 8394* (MO); *Lely Mountains; 175 kms SSE of Paramaribo, Mori, *Bolten 8575* (MO); *near airport, road Oelemari, *Boer 1047* (U); *Mapanegebied, *Elburg 9819* (U); *prope Jodensavanne, *Heyligers 438* (U); *Zuid River near Kayser Airstrip, *Irwin et al. 55978* (U); *Forest Reserve Zanderij, *Lanjouw 345* (GH); *Ribanau E of Moengo, *Lindeman 5889* (U), **Lindeman 6069* (U); *S of Moengo tapoe, *Lindeman 6162* (U); *W slopes of Bakhuis Mountains, *Florschütz & Maas 2924* (GH, U), **Maas 3094* (GH, U); Blakawatra, *Schulz 8645* (U). **FRENCH GUIANA.** Mathoury, Feb. 1901, *Lemme s.n.* (P); Karouany, 1855, *Sagot 423* (S, W); without locality, 1821, *Perrottet s.n.* (G), 1821, *Poiteau s.n.* (G); *above Taruni Creek, *Forestry Department of British Guiana 7495* (NY); *Tumuc–Humac, Frontière Bresil Guyane, *Granville 1378* (CAY); *N de Degrad Claude, *Granville 2204* (GH); *Chemin de Smerillons, a 5 km de Degrad Claude, *Granville 2224* (CAY); *Basse Ouaqui, au niveau de "Degrad Roche," *Granville B-4854* (CAY); *Saûl, Monts La Fumee, *Mori & Boom 14726* (F), **Mori & Boom 14834* (F), **Mori et al. 8767* (MO); *Haute Approuague, au confluent de la crique Parepou, *Oldeman B-1896* (CAY); *region of Tumuc–Humac, Massif du Mitaraka, *Sastre 1649* (CAY, P); *Haut Oyapock, Peola 20 km, en aval de Trois Sauts, *Sastre 4751* (P). **BRAZIL. Amapá:** Rio Oiapoque, islands of first cachoeira on Rio Iaue, 2°53′N, 52°22′W, 0.5 km E of confluence with Rio Oiapoque, 28 Aug. 1960, *Irwin, Pires & Westra 47900* (MG). **Pará:** Parque Indigena do Tumucumaque, Río Paru de Oeste, Missão Tiriyo, *Cavalcante 2518* (F); Belém, in sylvis ad Pará, May 1819, *Martius s.n.* (M); vicinity of Belém, Sep.–Oct. 1961, *Pires 51899* (NY, US); estrada do Cafezaldo IAN, 28 Oct. 1949, *N.T. da Silva 336* (GH, NY, P); Almeirim, Rio Arrayolos, 26 Apr. 1903, *Ducke s.n.* (MG, INPA); Oriximina, 8 Dec. 1906, *Ducke s.n.* (MG); Rio Cuminamirim, 16 Dec. 1906, *Ducke s.n.* (MG); Obidos, 10 Jan. 1920, *Ducke s.n.* (RB); Rio Branco, 21 Mar. 1924, *J.G. Kuhlmann 1722* (RB); Cachoeira do Rio Capim, 29 Jun. 1897, *Huber 887* (MG); *Belém, IPEAN, Reserva Mocambo, *Pires & Silva 10218* (GH, IAN), **Pires & Silva 11436* (GH); *Belem, IPEAN, *Schubert 2150* (US); *Rio Trombetas, planalto Saraca, *N.T. da Silva & Santos 4631* (F).

Brunfelsia guianensis was for a long time considered an anomalous species among the South American brunfelsias. With the recent discovery of several related species, it is now known to belong to a distinct section of the genus, of which it is the type species (Plowman, 1978). *Brunfelsia guianensis* differs from other species in this group

in having obovate leaves and a somewhat inflated, ovoid-campanulate calyx. The fruit is large and fleshy and yellow at maturity.

A lowland tropical forest species, *B. guianensisis* is distributed throughout the lower Amazon basin, chiefly north of the river, reaching well into the Guianas. It is known to flower from October to April, and fruits have been collected throughout the year. In the Brazilian state of Pará, this species is used in local medicine under the name *manaca* with properties similar to those of *B. uniflora* (see LeCointe, 1947; Plowman, 1977).

6. ***Brunfelsia martiana*** Plowman, Bot. Mus. Leafl. 24(20): 37. 1974. Type: BRAZIL. Provinciae Rio Negro (Amazonas): habitat in sylvis ad flum. Japura prope São João do Príncipe, Dec. 1819, *Martius 3247* (holotype, M; isotypes, M). **Figure 17.**

Shrub to 1 m tall. **Branches** few, naked below, somewhat knobby at nodes, glabrous. **Bark** cracked longitudinally, dark reddish brown, shiny, furnished with lenticels. **Leaves** scattered along branchlets, subsessile, blade 10–25 cm long, 4–8 cm wide, mostly oblong, sometimes elliptic-oblong or oblong-obovate, acuminate at apex, broadly cuneate to blunt at base, glabrous on both sides, upper surface dark green, nitid or dull, lower surface paler green, sometimes nitid, firmly membranaceous to subcoriaceous, midrib dark reddish brown, lateral nerves 8–12, spreading, straight; petiole very short, 1–4(12) mm long, glabrous, dark brown, becoming cracked, rugose. **Inflorescence** terminal or axillary in the upper leaf axils, glabrous, axis 2–10(15) mm long. **Flowers** 1–7 per inflorescence, sometimes with short peduncle that articulates with pedicel, greenish white to white. **Bracts** 1–3 per flower, 1–10 mm long, linear-lanceolate, concave, ciliolate at margin, caducous. **Pedicel** 3–6(10) mm long, short, slender, glabrous. **Calyx** 8–12 mm long, 3–8 mm in diameter, tubular to tubular-campanulate, glabrous, rarely striately veined, teeth 2–6 mm long, subequal, triangular-ovate to ovate-lanceolate, acute to acuminate at apex. **Corolla** tube 20–24 mm long, 1–3 mm in diameter, twice as long as calyx, straight, cylindric, inflated at apex, glabrous; limb 15–22 mm across, spreading, somewhat undulate, lobes 5–10 mm long, subequal, oblong-obovate, abruptly reflexed at lateral margins, rounded-subtruncate at apex. **Stamens** included within upper part of corolla tube; filaments subligulate, anterior pair 4 mm long, posterior pair 3 mm long; anthers about 1 mm in diameter, orbiculate-reniform, slightly unequal, the upper pair somewhat smaller. **Ovary** 2 mm long, oblong-ovoid; style about 15 mm long, filamentous, a little broader and curved at apex; stigma about 1 mm long, briefly bifid, upper lobe slightly larger. **Fruit** and **seed** incompletely known.

DISTRIBUTION—Guyana, Brazil (Amazonas, Bahía, Maranhão, Pará). See Figure 15.

SPECIMENS EXAMINED—**GUYANA.** Essequibo–Demerara River, Madray–Bubu Trail, Topy Trysil Forest, 8 Feb. 1944, *Forest Department 4422* (K). **BRAZIL. Amazonas:** Manaus and vicinity, road Manaus–Caracarai, km 22, 21 Mar. 1967, *Prance et al. 4704* (WIS); Rio Negro, Cachoeira Baixa de Tarumo, 11–14 Apr. 1973, *Schultes & Rodrigues 26132A* (ECON), *Schultes & Rodrigues 26133A* (ECON); *Mun. de Barcelos; Rio Demeni, *Fróes 28393* (IAN); *vicinity of Manaus, *Prance et al. 11611* (MO). **Bahía:** Dist. Ilhéus, Ferradas, Dec. 1818, *Martius s.n.* (M); Feira de Santana, Apr. 1850, *collector unknown* (G). **Maranhão:** Ilha São Luis; estrada que vai do Rio Anil para Maioba, *Fróes 25650* (IAN); Mun. Sta. Luzia; Fazenda Cacique, W of Sta. Inez and E of Entroncameento, *Taylor et al. 1084* (F). **Pará:** Faro, 22 Jan. 1910, *Ducke s.n.* (MG); Bella Vista, Rio Tapajoz, matta das immediacões da Campina do Perdido, 12 Feb. 1917, *Ducke s.n.* (MG); Região do Jutah y de Almerim. Palhal, 16 Apr. 1923, *Ducke s.n.* (RB); Gurupa, 25 Feb. 1923, *Ducke s.n.* (RB); Pará, May 1819, *Martius 3300* (M). **Without state:** *Schott 5361?* (W), *Schott s.n.* (W).

Brunfelsia martiana belongs to section *Guianenses*. The type specimen collected by Martius (*Schedulae 3247*) on the Rio Japura includes a handwritten description of the plant that Martius apparently intended to publish as *B. acuminata*, a name that was later used by Pohl and Bentham for a form of *B. brasiliensis*.

Brunfelsia martiana has been very poorly collected, as is true of many of the species of section *Guianenses*. The few collections available were collected over an extensive geographical area spanning the entire breadth of Brazil, and nearly all are preserved in European and Brazilian herbaria. The species has been collected only twice in the last 50 years; no collections have been made in the state of Bahía since 1850. One apparently quite early collection with six duplicates is preserved in Vienna. The label bears only the data "*Schott 5361*, Brasilia." This appears to be

FIG. 17. *Brunfelsia martiana*. Reproduced courtesy of the Botanical Museum of Harvard University.

the wrong label for the specimen because Schott collected only in the state of Rio de Janeiro and no other collection of the species has ever been made there. Mislabeling of the collections of Schott and Pohl has been recognized since the time of Martius, who made a special note of it in *Flora Brasiliensis* [**1**(1): 82 (1906)]: "Dolendum quod, quae specimina a cl. POHL, quae a cl. SCHOTT collecta sint, ex plagulis herbarii palatini Vindobonensis non semper statui potest."

The origin of this collection remains questionable, yet it must be taken into consideration because it represents one of the more complete gatherings of the species and includes an immature fruit.

Brunfelsia martiana is a small shrub with greenish white flowers. It is related to both *B. amazonica* and to *B. guianensis* and occurs sympatrically with both of these species. *Brunfelsia martiana* differs from *B. amazonica* in having larger leaves (10–25 vs. 6–12 cm) with more lateral nerves (8–12 vs. 5–8) and much shorter pedicels (3–6 vs. 13–20 mm).

Brunfelsia martiana is closely allied with *B. guianensis* as well, and specimens of the former were originally considered to be exceptional forms of *B. guianensis*. Additional material proved the distinctiveness of *B. martiana*. It is now distinguished from *B. guianensis* by having larger (10–25 vs. 6–15 cm), oblong leaves with more lateral nerves (8–12 vs. 4–5), a calyx that is usually narrow-tubular instead of ovoid-campanulate, and a corolla tube that is rarely more than twice as long as the calyx. In *B. guianensis* it is frequently 2½–3 times as long.

The flowers of all three of these related species are remarkably similar in the shape and color of the corolla, especially in the curious form of the corolla lobes, the lateral margins of which are deflexed, giving them a rectangular appearance. The fruit of *B. guianensis* is a thick-walled, fleshy capsule; that of *B. amazonica* is thin-walled and dry at maturity. The collection labeled *Schott 5361* mentioned above includes a small, immature fruit enclosed by a coriaceous and striately veined calyx. The pericarp appears cartilaginous but not fleshy in this early stage.

A second collection, which for *B. martiana* has exceptionally small leaves reminiscent of *B. guianensis*, was made by Martius near Belém do Pará. This specimen included the remnants of a fruit that is small, definitely thin-walled, and brittle, perhaps the remains of the endocarp only. Martius tentatively named this plant *B. flexuosa* and wrote a description (*Schedulae 3300*) that appears on the same page attached to the type specimen of *B. martiana*. The nature of the fruit in this species remains problematical. When, indeed, it is fully known, it should be very useful in determining the relationship of *B. martiana* to other species.

Brunfelsia martiana is one of the most widely distributed species of section *Guianenses*, growing in tropical lowland forests from Guyana south to Bahía in Brazil and westward to the Colombian frontier. The curious distribution between the Amazon basin and the coastal forests of Bahía has been observed in other groups of plants (Plowman, 1979).

Brunfelsia* sect. *Franciscea (Pohl) Griseb., Fl. Brit. W. I.: 432. 1861. *Franciscea* Pohl, Pl. Bras. Icon. Descr. 1: 1, t. 1–7. 1826. Lectotype species (designated here): *Franciscea uniflora* Pohl.

TYPE SPECIES—*Brunfelsia uniflora* (Pohl) D. Don, Edinburgh New Philos. J. 86. Jul. 1829.

Shrubs or small trees, 0.3–10 m tall. **Inflorescence** terminal, rarely axillary. **Flowers** large or small, 1–many per inflorescence. **Corolla** purple fading to pale violet or white with age, with white eye at mouth, tube 1–4 times as long as calyx, slightly inflated near apex, then slightly constricted to form thickened ring, the lobes broadly rounded, overlapping at lateral margins. **Stigma** briefly bifid, in the form of a forceps. **Anthers** orbicular-reniform in outline. South and Central America.

Note: Pohl, in establishing his new genus *Franciscea*, included seven species. In recognizing this name as a section of *Brunfelsia*, it is necessary to designate a type species. I have chosen *B. uniflora* (Pohl) D. Don for the following reasons. It is the oldest known species of the genus, having appeared in 1648 in the work of Piso under the name *Manacá,* accompanied by a good illustration showing the flowers and fruits (Fig. 18). The holotype collected by Pohl and preserved in Vienna is a reasonably good specimen showing the characters of the species. The species is one of the most widespread of the genus and is well represented in herbaria. Lastly, *B. uniflora* (as *B. hopeana*) was the only species mentioned by Grisebach (1861) in setting up *Franciscea* as a section of *Brunfelsia*.

FIG. 18. Manacá (*Brunfelsia uniflora*). From Piso, W., De Medicina Brasiliensis (1648).

Although the date 1827 appears on the title page of Pohl's work *Plantarum Brasiliae Icones et Descriptiones*, it has been pointed out (Stafleu, 1967; Stafleu & Cowan, 1983) that the first part of the work, including the text and plates of *Franciscea*, actually appeared in August 1826.

7. ***Brunfelsia australis*** Benth. in DC., Prodr. 10: 200. 1846. Lectotype (designated by Hunt, 1978): BRAZIL. Brasilia meridionalis, Rio Uruguay, *Baird s.n.* (K). Lectoparatypes: ARGENTINA. Buenos Aires, in hortis Bonariensibus sub nomine Jasmini Paraguayensis culta, *Tweedie s.n.* (K); Estrada de Minas, *Martius s.n.* (?). No collection of Martius with this data has been located. Query was made by Bentham. *Sellow 1573*, also cited by Bentham, is excluded as a type; it belongs to *B. pilosa* Plowman. **Figure 19.**

Franciscea australis (Benth.) Miers, Ann. Mag. Nat. Hist. ser. 2, 5: 250. 1850.

Brunfelsia hopeana var. *australis* (Benth.) J.A. Schmidt in Mart., Fl. Bras. 8(1): 262. 1864.

Brunfelsia paraguayensis Chodat, Bull. Herb. Boissier, ser. 2, 1: 406. 1901. Type: PARAGUAY. In silvis pr. Río Apa, May, without year, *Hassler 725a* (holotype, G).

Brunfelsia uniflora f. *typica* Hassl., Feddes Repert. Spec. Nov. Regni Veg. 15: 243. 1919. *Non sensu* D. Don. Type: PARAGUAY. In silvis pr. Río Apa, May, without year, *Hassler 725a* (holotype, G).

Brunfelsia uniflora f. *obovatifolia* Hassl., Feddes Repert. Spec. Nov. Regni Veg. 15:243. 1919. Type: PARAGUAY. Cordillera de Altos, in silvis, frutex vel arbor parva 3–5 m, corolla albo-coerulescens vel violacea in eadem planta, Sep. 1898–1899, *Hassler 3246* (holotype, G; isotypes, A, G, NY, P, W).

Brunfelsia uniflora f. *intermedia* Hassl., Feddes Repert. Spec. Nov. Regni Veg. 15: 243. 1919. Lectotype: PARAGUAY. In regione lacus Ypacaray, Cordillera do Altos, arbusto 2–2.5 m, fl. lila-morado, montes y orillas, cordilleras y bajos, *azucena*, Sep. 1913, *Hassler 12257* (lectotype, G; isolectotypes, C, GH, K, L, MO, NY). Lectoparatypes: PARAGUAY. In regione lacus Ypacaray. Picada a Bernalcue, Mar. 1913, *Hassler 12147* (A, G); San Bernardino, orillas montes, fl. morado despues blanca, arbusto 3–4 m, Aug. 1915, *Hassler* (cited as *Rojas*) *1333* (G).

Shrub to small tree 2–4 m tall. Trunk often branched from near base, to 8 cm in diameter. **Bark** rugose, yellowish brown. **Branches** ascending and spreading, leafy, glabrous, green with yellowish brown cracks, furnished with lenticels. **Branchlets** glabrous, green. **Leaves** scattered along branchlets, blade 4.0–12.5 cm long, 2.5–6.0 cm wide, broadly elliptic to obovate, rarely orbicular or rhombic, blunt to rounded at apex, occasionally acute, cuneate at base, often briefly pubescent-ciliate when young, becoming glabrous, or sparsely glandular beneath at costa, dull dark green above, pale green beneath, membranaceous to subcoriaceous, lateral nerves 5–7, prominulous beneath, straight or somewhat arching, veinlets often obscure; petiole 3–8 mm long, glabrous or sparsely pubescent. **Inflorescence** terminal at the tips of the branchlets, sessile, with 1–4 flowers. **Bracts** present or absent, to 2 mm long, lanceolate, concave, ciliolate, early caducous. **Flowers** showy, violet, fading to pure white with age, fragrant. **Pedicel** stout, 4–7 mm long, glabrous, becoming thicker and corky-verrucose in fruit. **Calyx** 7–12 mm long, 4–10 mm diameter, campanulate, more or less inflated, glabrous, rarely papillose-punctate, pale green, firmly membranaceous, reticulately veined, teeth 3–6 mm long, ovate-lanceolate, acute; calyx in fruit coriaceous, partially enclosing fruit, smooth. **Corolla** tube 25–32 mm long, 1.5–2.0 mm in diameter, 2–3 times as long as calyx, glabrous, often sparsely glandular in bud, glabrescent; limb 30–40 mm in diameter, plane, spreading, thickening at mouth prominent, round, white or yellowish, lobes equal, broadly rounded, overlapping laterally, abruptly narrowed at base. **Stamens** included; filaments slender, upper pair 2–3 mm long, lower pair 3–5 mm long; anthers about 1 mm in diameter, reniform-orbicular. **Ovary** 2.5 mm long, 1 mm in diameter, ovoid-conical; style 20–28 mm long; stigma about 1 mm long. **Capsule** 10–22 mm long, 10–20 mm in diameter, subglobose to ovoid, apiculate at apex, smooth, glabrous, dark green, pericarp to 0.5 mm thick, dry at maturity, indehiscent or tardily dehiscent. **Seeds** 20–40, 4–6 mm long, 3–4 mm in diameter, oblong-ellipsoid, angular, dark brown. **Embryo** 3–4 mm long, slightly curved; cotyledons ovate.

DISTRIBUTION—Brazil (Paraná, Rio Grande do Sul, São Paulo), Paraguay, Argentina (Chaco, Corrientes, Formosa, Misiones, Santa Fé), and Uruguay; cultivated in some areas, especially in Central America. See Figure 20.

SPECIMENS EXAMINED—**BRAZIL. Paraná:** *Municipio Foz do Iguaçu; Vila Postes, *Buttura 157* (F); *Ceu Azul, *Hatschbach 43192* (F). **Rio Grande do Sul:** Neu Wurttemberg, 450 m, 15 Oct. 1904, *Bornmuller 219* (A, G, GH, M, W); São Leopoldo, 16 Oct. 1934, *Rambo 321* (C); Porto Alegre, 12 Sep. 1945, *Rambo 37819* (A, C, W);

Morra da Glória, *Rambo 29147* (BR, MO). *Municipio Itaqui, *Dobereiner & Tokarnia 841* (RB). **São Paulo:** *Parque Estadual do Turvo, Tenente Portela, Paiva, *Stehmann s.n.* (F). **PARAGUAY. Cordillera de Altos:** Cerros de Tobatí, 18 Aug. 1902, *Fiebrig 49* (A, F, G, L, M, PR); *Hassler 725* (G); Sep. 1913, *Hassler 12559* (A); Villarrica, Sep. 1931, *Jorgensen 3661* (A, C, F, MA, MO, NY, PH, S, US); Dep. Cantera, Zona Grande Bosques, Herrera Vegas, 220 m, 11 Aug. 1939, *Montes 4703* (BAB); Dep. San Pedro, Colonia Primavera, 11 Sep. 1955, *Woolston 571* (C, GH, NY, S, UC); without locality, 26 Aug. 1874, *Balansa 2240* (G, GOET, K, LD, LE, PE, S); 4 Sep. 1854, *Palmer 155* (US); *Paraguarí, Cerro San Jose, a civitate Ybicui, *Bernardi 18138* (F); *Neembucú, Curupaity ad Laureles, *Bernardi 20495* (F). **ARGENTINA. Chaco:** Dep. Resistencia, Margarita Belen, 8 Sep. 1946, *Aguilar 841* (S), 18 Sep. 1948, *Aguilar 1302* (W); Dep. Primer de Mayo, Colonia Benitez, Oct.–Nov. 1928, *Schulz 85* (BAB), 26 Nov. 1906, *Stuckert 16307* (G); Las Palmas, *Jorgensen 2098* (GH, MO, UC); Río de Oro, km 140 de Resistencia, 29 Aug. 1944, *Rojas 12133* (UC). **Corrientes:** Capital, Feb. 1821, *Bonpland 528* (P); 1908, *Llamas s.n.* (BAB); Quinta La Eloisa, 77 m, 6 May 1969, *Plowman 2713* (ECON, GH). Dep. Concepción, Tabay, 1 Nov. 1965, *Krapovickas & Cristobal 11706* (UC); 7 June 1969, *Krapovickas & Cristobal 15385* (C, MO); 7 May 1969, *Plowman 2723* (ECON, GH); Dep. Mburucuyá: Estancia "Santa Teresa," 6 Sep. 1949, *Pedersen 418* (BR, C, GH, P, S, US); Estancia "Santa Maria," Campo "Dios Gracia," 18 Dec. 1949, *Pedersen 418* (BR, C, NY, P, S); Estancia Santa Ana, 21 Oct. 1944, *Schwarz 93* (A); Cañada Paso Clarios, 11 Nov. 1949, *Schwarz 8661* (BH, G, W). Dep. Bella Vista, Bella Vista, Oct. 1904, *N. Rojas Acosta 13004* (BAB); Dep. Saladas: Laguna Salada, 28 Sep. 1944, *Schwarz 36* (A); Laguna Soto, 28 Sep. 1944, *Schwarz 48* (A); Paso del Deseo, 1 Nov. 1944, *Schwarz 139* (A, UC); 2 Dec. 1949, *Schwarz 8972* (BH, G, W). Dep. Ituzaingo, Salto Apipe, 6 Oct. 1949, *Schwarz 8114* (BR); Dep. Generál Paz, Laguna Rincón, 2 Nov. 1949, *Schwarz 8547* (LD); Dep. San Roque, San Roque cercanías, 20 Apr. 1945, *Ybarrola 2963* (UC, W); Dep. San Luiz del Palmar, Colonia J. M. Llano, 19 Sep. 1945, *Ybarrola 3270* (B, W); Cerrudo Cue, 5 Sep. 1946, *Ybarrola 3430* (G, P); vicinity of Goya, 15–30 m, 2–10 Nov. 1913, *Curran s.n.* (US); *Dep. Santo Tomé, Garruchos, *Krapovickas et al. 26092* (MO); *Dep. San Martín, Carlos Pellegrini, *Krapovickas 29261* (MO); *Dep. San Martín, *Sussini, Schinini et al. 18580* (F). **Formosa:** Dep. Pilcomayo, Estancia Riacho Negro, 3 Oct. 1947, *Morel 3783* (BR, MO); Salvación, 17 Nov. 1947, *Morel 4144* (C); S.O. a 12 km de Filipina, Est. Salaberry, 21 Nov. 1949, *Morel 8921* (BH, C, G, W); Formosa, 29 Oct. 1900, *Kermes 1363* (BAB); Fontana, Aug. 1933, *Meyer 166* (GH). **Misiones:** Dep. Iguazú, Salto Iguazú, 2 Oct. 1947, *Pierroti 6563* (G); 6 Oct. 1910, *Rodriguez 484* (A, US); Dep. Candelária, Martires, 24 Oct. 1917, *Bertoni 3434* (W); Loreto, 26 Sep. 1932, *Muniez 99* (BAB); Dep. San Javier, Acaragua, 16 Sep. 1946, *Bertoni 2939* (B); Dep. G. M. Belgraw, "El Caburei," 450 m, 22 Sep. 1957, *Montes 27471* (M, NY); without locality, *Fox s.n.* (CGE). **Santa Fé:** Dep. General Obligado, Florencia, 30 Oct. 1923, *Chiar s.n.* (BAB); Villa Guillermina, 14 Feb. 1939, *Ragonese 3646*, (F); Indio Muerto, 6 Mar. 1939, *Meyer 3076* (A). **URUGUAY.** Banda Oriental, 1816–1821, *St. Hilaire C-2197* (P).

CULTIVATED SPECIMENS OF INTEREST—**BRAZIL. Rio Grande do Sul:** Porto Alegre, 20 Mar. 1893, *C. Lindman A597a* (S); Santa Maria, Silvacultura, 14 Oct. 1955, *Michel 8* (B). **Rio de Janeiro:** Rio de Janeiro, Quinta de Boa Vista, 13 Oct. 1879, *Glaziou 12110* (BR, C, G, LE, P, R); Rio de Janeiro, Oct. 1915, *Vincent s.n.* (L). **Santa Catarina:** Brusque, 4 Oct. 1961, *Reitz & Klein 11250* (US). **ARGENTINA. Tucumán:** Capital, Instituto Lillo, 9 Sep. 1947, *Meyer 12621* (B); Dep. Trancaas, San Pedro de Colalao, 1,200 m, Apr. 1926, *Venturi 4408* (A).

Bentham described *B. australis* from three specimens, two of which are included in the present concept. *Baird s.n.* was chosen (by Hunt, 1978) as the lectotype. One of the other specimens, collected by Tweedie, was made from horticultural material in Buenos Aires. The third collection cited by Bentham, *Sellow 1573*, is here referred to *B. pilosa*, a closely allied species. A fourth collection by Martius (with a query by Bentham) cannot be located. The locality "Estrada de Minas" indicates another species was involved because *B. australis* does not occur north of Rio Grande do Sul in Brazil.

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FIG. 19. *Brunfelsia australis*. Reproduced courtesy of *Curtis's Botanical Magazine* and Christabel King.

Brunfelsia australis CHRISTABEL KING *del.*

FIG. 20. Distribution of *Brunfelsia australis* (solid triangle), *B. boliviana* (solid square), and *B. bonodora* (solid circle).

Schmidt in Martius (1864) considered *B. australis* to be a variety of *B. uniflora* (*B. hopeana*). He cited the Sellow collection mentioned above and two additional specimens. One of these, *Riedel s.n.*, collected near Macaé, Rio de Janeiro, agrees with *B. bonodora*. The other collection, *Martius s.n.*, from Pará, is referred to *B. guianensis*, although most of this material is sterile.

Brunfelsia australis is closely related to *B. uniflora* and *B. pilosa* and by some authors (Schmidt 1864; Hassler, 1919) has been considered synonymous with *B. uniflora*. However, these workers suffered from the disadvantage of working exclusively with dried herbarium specimens (Schmidt) or with local populations without understanding the entire morphological range of the species involved (Hassler). Studies of both *B. australis* and *B. pilosa* in the field and of all three entities in cultivation and from herbarium specimens reveal that these plants are morphologically, ecologically, and geographically distinct and merit the rank of species. Experimental crosses suggest that reproductive isolation exists between *B. pilosa* and *B. australis*.

Brunfelsia australis is distinguished from *B. uniflora* and *B. pilosa* by the broadly elliptic to obovate leaves, the variable number (one to four) of flowers per inflorescence and the uniformly glabrous, campanulate calyx.

Even though their ranges overlap, almost no intermediates have been found between *B. australis* and *B. pilosa*. One collection from Rio Grande do Sul, *Bornmuller 219*, has oblong leaves and a more deeply incised calyx and may represent

some introgression from *B. pilosa*, which also occurs in this region.

Commonly growing as a tall shrub or treelet, *B. australis* is found primarily in the relatively recent drainage systems of the Rio Paraná, Rio Uruguay, and Rio Jacuí (Rio Grande do Sul), growing in the understory of low-elevation forests near the rivers and in adjacent uplands. It occurs from sea level to 450 m altitude. In the low-lying, often swampy river basin of the Rio Paraná, *B. australis* is found in the scattered woodlands that appear on higher and drier ground.

Two reports of widely disjunct populations are now known to represent cultivated plants. *Venturi 4408* from Tucumán, Argentina, was distributed to some herbaria without the notation "culta." Specimens of *Glaziou 12210* were distributed with the fictitious provenance "Rio de Janeiro, Serra da Palmital." However, a duplicate specimen at the Museu Nacional de Rio de Janeiro bears the correct locality, "Quinta da Boa Vista (Rio), Arbusto cult." This erroneous data may be the result of direct falsification by Glaziou, which was pointed out in the Melastomataceae by Wurdack (1970).

Brunfelsia australis flowers from August to November; mature fruits appear from April to June. Frequently the entire plant is covered with fragrant, showy purple and white flowers at the same time, making this species a valuable ornamental. It is widely cultivated in gardens between latitudes 35°N and 35°S (San Francisco, California, to Buenos Aires, Argentina).

8. *Brunfelsia boliviana* Plowman, Fieldiana, Bot. n.s. 8:1. 1981. Type: BOLIVIA. Santa Cruz: Prov. de la Cordillera, region of Lagunillas, Cordillera of Incahuasi, 900 m, "at dry and sandy slopes; shrub 1–2 m; flowers white or light violet; when cattle eat the leaves of this plant [they] die." N. v. *bella unión*. Aug. 1934, *Cárdenas 2813* (holotype, F 756420). **Figure 21.**

Shrub 1–2 m tall (fide Cárdenas). Bark on branches thin, yellowish to grayish brown, longitudinally rugose, not exfoliating. **Branchlets** 2–3 mm in diameter, more or less villous, becoming glabrous. **Leaves** scattered along branchlets or crowded at tips of lateral short shoots, 40–135 mm long, 23–58 mm wide, blade obovate, rarely elliptic-obovate, apically rounded with a short acumen 5–10 mm long, the acumen itself blunt to acute, somewhat revolute at margin, basally attenuate, glabrescent on both surfaces except at the midrib, which bears villous and glandular hairs, ciliate-villous on the adaxial surface of the revolute margin, dull green above, paler, yellowish green beneath, firmly membranaceous or somewhat coriaceous, the lateral nerves 4–9, straight, arcuately anastomosing toward the margin, prominulous beneath; petiole short, 2–6 mm long, more or less villous, more densely so on upper side. **Inflorescence** corymbiform, terminal on last season's branchlets, short pedunculate, branched, with 6–15 flowers. **Peduncle** 5–12 mm long, more or less villous. **Bracts** small, 14 mm long, lanceolate or cymbiform, sparsely to densely villous especially at margin, caducous. **Flowers** light violet fading to white (fide Cárdenas). **Pedicel** short, 2–6 mm long, 1 mm in diameter, scarcely thickened at apex, glabrous or with sparse glandular hairs. **Calyx** 9–15 mm long, 3–4 mm in diameter, tubular, truncate at base, 5-angled in cross section, appearing plicate in pressed specimens, glabrous or with scattered glandular hairs, teeth 2–4 mm long, subequal, ovate, apically short acuminate, the acumen itself blunt and glandular-papillose; fruiting calyx persistent, withering. **Corolla** tube 21–25 mm long, 2–3 mm in diameter, about twice as long as calyx, straight; limb 18–30 mm in diameter, spreading, lobes 8–14 mm long, subequal, rounded. **Stamens** inserted in upper part of corolla tube; filaments strap-shaped, the anterior pair 3 mm long, suberect, briefly exserted from mouth of corolla tube, the posterior pair 2 mm long, included; anthers 1–1.2 mm in diameter, orbicular-reniform, subequal or the upper pair slightly larger. **Ovary** 2–3 mm long, 1.8–2.2 mm in diameter, narrowly ovoid, with about 30 ovules; style 19 mm long, incurved at apex; stigma 2 mm long, briefly bifid. **Capsules** 3–6 per infructescence, 20–25 mm long, 20–25 mm in diameter, dry at maturity, subglobose, smooth, green; pericarp thin, 1–1.5 mm thick, endocarp thin, crustaceous, with 22–28 seeds per capsule. **Seeds** 5–8 mm long, 2–3 mm in diameter, oblong to subreniform, subterete, dark brown, reticulate-pitted. **Embryo** 4 mm long, straight; cotyledons 1.5 mm long, ovate; radicle 2.5 mm long.

DISTRIBUTION—The eastern Andes of southern Bolivia. See Figure 20.

SPECIMENS EXAMINED—**BOLIVIA. Chuquisa-**

BRUNFELSIA boliviana *Plowman*

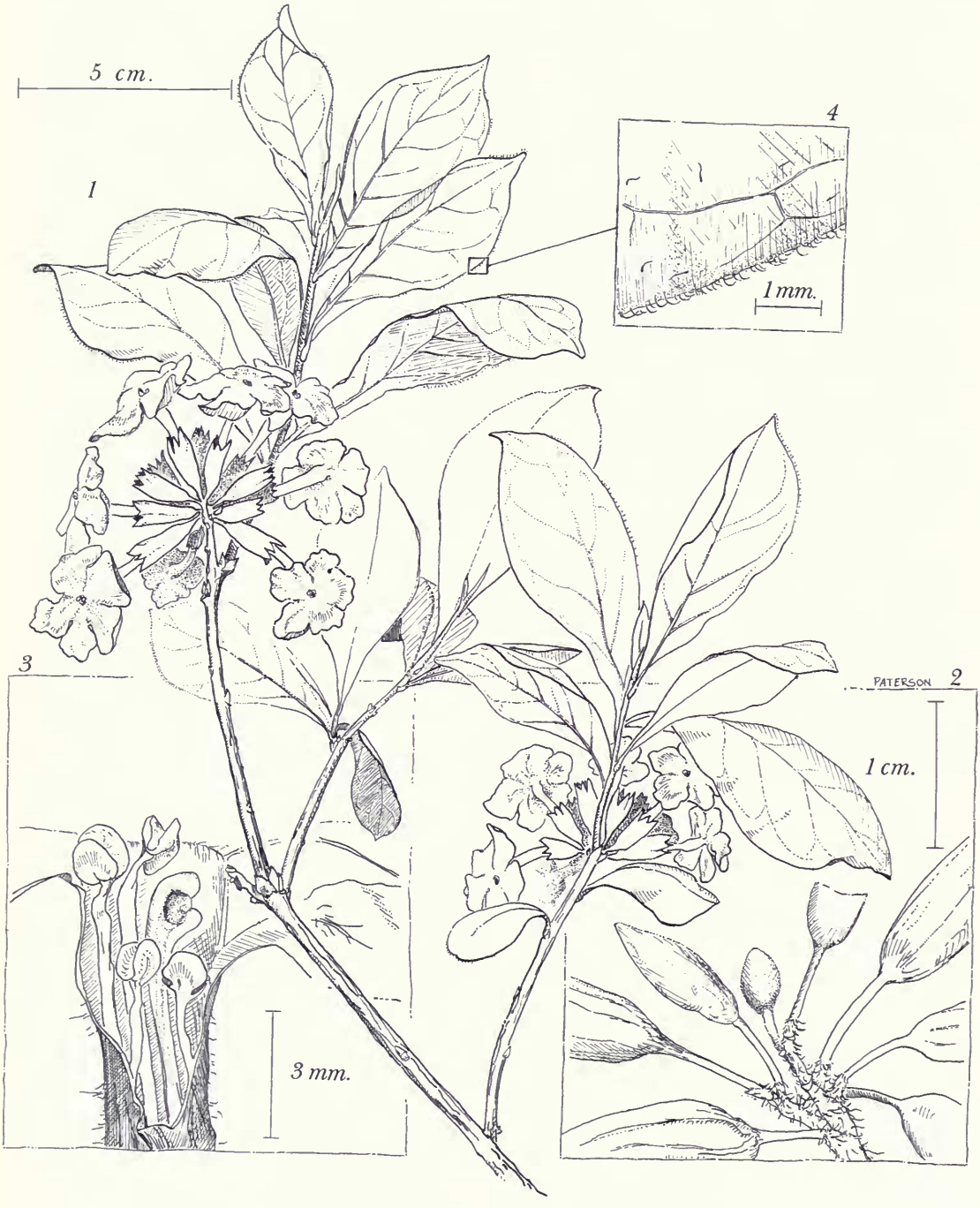

FIG. 21. *Brunfelsia boliviana*. Reproduced courtesy of the Field Museum of Natural History.

ca: mountain above Bartolo, on road from Monteagudo to Sucre, 20°00′S, 64°45′W, 5000 ft, 20 Sep. 1949, *Brooke 5653* (BM). **Santa Cruz:** Prov. Cordillera, Nov.–Dec. 1845, *Weddell 3621* (P, 2 sheets); 5 km N of Yatarenda, 63°32′W, 19°12′S, 17 Apr. 1977, *Krapovickas & Schinini 31476* (CTES, F); *Prov. Luis Calvo: Monteagudo 26 km hacia Camiri, *Beck & Liberman 9379* (F).

Brunfelsia boliviana is known from only five collections, all from a relatively small area in the foothills of the Andes in southern Bolivia. The early collection of Weddell in 1845 is labeled merely "Provincia de la Cordillera," referring to the large province in the department of Santa Cruz. However, Urban (1906) mentions that in the months given, Weddell traveled and collected from Santa Cruz da la Sierra in Santa Cruz south to Sauces (now Monteagudo) in the department of Chuquisaca. His collection was probably made near the border between the two departments.

Brunfelsia boliviana is most closely related to *B. cuneifolia*, which occurs in southern Brazil from the state of Paraná south to Rio Grande do Sul. Like the present species, it is known from only a few specimens. *Brunfelsia boliviana* differs in both leaf and inflorescence characters as summarized in Plowman (1981).

The geographical distribution of these two closely related species deserves some comment because it exemplifies further a pattern observed in other brunfelsias in which vicarious species pairs are found in southeastern Brazil and the eastern Bolivian Andes. These include *B. bonodora–B. grandiflora* subsp. *schultesii* and *B. hydrangeiformis–B. mire*. In addition, disjunct and somewhat distinct populations of *B. uniflora*, a species primarily of eastern Brazil, have also been found in the Bolivian Andes. In each of these cases, vicarious species or populations are now separated by more than 2,000 km in which no intervening populations are known to occur. This phytogeographical pattern has been discussed by Smith (1962) and by Plowman (1979).

Interestingly, the leaves of *B. boliviana* are reputed to be lethal to cattle, a feature that has been reported for other *Brunfelsia* species (Plowman, 1977).

9. *Brunfelsia bonodora* (Vell.) J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13, 5-B(1): 152. 1962. **Figure 22.**

Besleria bonodora Vell., Fl. Flumin. 261. 1829 ("1825"). Ic. 6, t. 80. 1831 ("1827"). Lectotype (designated here): Vellozo, J.M. da C., Fl. Flumin. Ic. 6, t. 80. 1831 ("1827"). Representative collection: BRAZIL. Rio de Janeiro, Serra de Estrella, Mar. 1833, *Riedel 84* (LE).

Shrub 1–2 m tall. **Branches** ascending, spreading, naked, glabrous. **Bark** thin, light brown. **Branchlets** glabrous or sparsely puberulent, grayish brown. **Leaves** scattered along branchlets, blade 5–14.5 cm long; 2–5 cm wide, narrowly elliptic to lanceolate, acuminate at apex, blunt to cuneate at base, glabrous, at times puberulent at midrib on lower surface, shiny, dark green on upper surface, pale green beneath, firmly membranaceous, lateral nerves 5–8, more or less arcuate; petiole 2–6 mm long, slender, glabrous. **Inflorescence** terminal, compact, unbranched, axis 3–8 mm long. **Flowers** 3–15, rarely reduced to 1 or 2; blue fading to white with age, fragrant. **Bracts** 2–12 mm long, lanceolate, glabrous or puberulent, caducous. **Pedicel** 6–12 mm long, slender, thickened slightly at apex, glabrous. **Calyx** 11–14 mm long, about 5 mm in diameter, tubular-campanulate to campanulate, ellipsoid to obovoid in bud, rarely somewhat inflated, glabrous, firmly membranaceous, striately veined, teeth 3–4 mm long, triangular to ovate, acute to blunt at apex, rarely apiculate, calyx to 15 mm long in fruit, subcoriaceous, conspicuously veined, enclosing fruit. **Corolla** tube 17–25 mm long, 2 mm in diameter, twice as long as calyx, glabrous or sparsely glandular; limb 20–35 mm in diameter, plane spreading, lobes rounded to oblong, subtruncate or rounded at apex, rarely emarginate, overlapping at sides, narrowed abruptly at base. **Stamens** included in upper part of corolla tube; filaments about 4 mm long, subligulate; anthers 1.5 mm long, reniform. **Ovary** 1.5 mm long, ovoid-conical; style slender, equaling the filaments; stigma 1 mm long, briefly bifid, upper lobe slightly larger, obtuse. **Capsule** 8 mm long, 6–8 mm in diameter, partially enclosed by calyx, ovoid-turbinate, apiculate at apex, smooth, pericarp thin-walled, drying crustaceous, sparingly dehiscent. **Seeds** about 5, incompletely known.

DISTRIBUTION—Brazil (Rio de Janeiro, São Paulo). See Figure 20.

SPECIMENS EXAMINED—**BRAZIL. Rio de Janeiro:** Serra de Estrella, 700 m, 29 Oct. 1946, *Brade 18643* (RB), 12 Nov. 1823, *Riedel 18* (A, LE, mixed collection; NY, mixed collection; US), 14 Dec. 1823, *Riedel 59* (A, LE, mixed collection);

Didyn. Angiosp.

BESLERIA BONODORA

(Tab. 80.)

Macahé, May 1832, *Riedel sp. nov.* (LE); Barra Mansa, Fazenda Paraiso, 3 Dec. 1960, *Duarte 5477* (RB, US). **São Paulo:** Taubate, Dec. 1817, *Martius 541* (M). **Without state:** *Riedel 112* (US).

Brunfelsia bonodora was first described in the genus *Besleria* by Vellozo in *Flora Fluminensis*, a work that appeared in 1829 although 1825 appears on the title page (Carauta, 1973). Vellozo's scanty description was accompanied by a somewhat stylized illustration. This drawing must now be considered the lectotype of the species since no specimens of Vellozo exist (Fig. 22).

In his monograph of *Brunfelsia* in 1846, Bentham erroneously placed Vellozo's species in synonymy with his *B. latifolia* (based on *Franciscea latifolia* Pohl). This concept also included material now recognized as *B. grandiflora* subsp. *schultesii* of the western Amazon and Andes. This problem was discussed by Monachino (1953) and Macbride (1962), but neither of these workers were able to resolve the issue, primarily because they saw neither the type materials nor representative collections from southeastern Brazil.

It is now clear that the name *B. latifolia* and its synonym, *B. maritima* Benth., apply to a distinct species known only from the sand *restingas* around the city of Rio de Janeiro. *Brunfelsia bonodora* is represented by several collections from the mountains of the state of Rio de Janeiro that agree with Vellozo's description and plate. This concept is, however, not identical with Macbride's interpretation of the species since he included material here referred to as *B. grandiflora* subsp. *schultesii*.

Nevertheless, *B. bonodora* is related to both *B. latifolia* and *B. grandiflora* subsp. *schultesii*, which is in part responsible for the confusion of these concepts. *Brunfelsia bonodora* is distinguished from *B. latifolia* in having a more robust, upright habit; longer, lanceolate, and apically acuminate leaves; and longer pedicels. In addition, *B. bonodora* differs ecologically, growing in the montane rain forests of the Serra do Mar and not in open, coastal formations (*restingas*). There seems to be some overlap in these two species, but the status of possible hybrids cannot be determined with so few specimens at hand, most of which lack adequate collection data. In fact, only two modern collections of *B. bonodora* are known.

Macbride (1962) considered *B. bondora* to be conspecific with the plant here treated as *B. grandiflora* subsp. *schultesii*. On close examination, however, there are several points of difference between them. *Brunfelsia bonodora* has longer pedicels (6–12 vs. 2–5 mm), a more compact inflorescence, larger bracts, and the capsule almost completely enclosed by the calyx in fruit. According to the specific epithet, *B. bonodora* is fragrant; *B. grandiflora* almost never is.

Geographically, *B. bonodora* and *B. grandiflora* are separated by several thousand miles. They exhibit, however, a distribution similar to those of *B. hydrangeiformis* and *B. mire* and may be considered to be vicarious species that arose from a common ancestor. *Brunfelsia bonodora* is known only from the coastal montane rain forests in the state of Rio de Janeiro, at elevations up to 700 m. It flowers from October to December and fruits during May and June. Additional collections of this plant with complete field data will greatly aid in understanding its specific characters and relationships.

10. *Brunfelsia brasiliensis* (Spreng.) L. B. Sm. & Downs in Reitz, Fl. Ilustr. Catar., pt. 1, Sola: 303. 1966.

Gerardia brasiliensis Spreng., Syst. Veg. 2: 806. 1825. Type: BRAZIL. Brasilia meridionalis, without locality, *Sellow s.n.* (type destroyed at Berlin; representative collection and possible isotype, M).[12]

Shrub 0.3–2 m tall. **Bark** roughish, reddish to light brown. **Branches** numerous, arising from near base, leafy, yellowish brown, pilose, especially so when younger, or glabrous. **Branchlets** of current year leafy, slender, erect, densely pubescent with yellowish brown, nonglandular hairs. **Leaves** scattered along branchlets, sometimes more crowded toward apex, blade 3–13 cm long, 1–4.5 cm wide, lanceolate to oblong-lanceo-

[12] In the manuscript Plowman gave no obvious indication that he wished to lectotypify this species as cited. We have thus left the lectotypification of this species to later *Brunfelsia* specialists.—*Eds.*

←

FIG. 22. Lectotype of *Brunfelsia bonodora* (originally as *Besleria bonodora*). From Vellozo, J. M. C., Flora Fluminensis (1881).

late, more rarely obovate-oblong, acute to acuminate at apex, occasionally blunt, cuneate to narrowed at base, the upper surface sparingly pubescent, dark to light green, rarely nitid, subscabrous or glabrate, the lower surface variously pubescent, often villous at midrib, rarely glabrous, paler green, firmly membranaceous to coriaceous, lateral nerves 6–10, mostly straight; petiole 1–5 mm long, puberulent to villous. **Inflorescence** terminal and subterminal, corymbiform, compact and nearly sessile or lax-elongate, with 5–many flowers, rarely reduced to 1–2, the axis 1–2 cm long, pubescent-villous. **Bracts** small, 2–15 mm long, lanceolate, ciliolate at margin, pubescent, caducous. **Flowers** often showy, violet fading to pale lavender or white with age, odorless, short pedunculate. **Peduncles** 2–8 mm long, thickened at apex and articulating with pedicel, persistent, villous or glandular-pubescent, bearing 1–3 bracts. **Bracts** minute, 1–2 mm long, linear-lanceolate. **Pedicel** 2–15 mm long, erect, pubescence yellowish to yellowish brown, sparsely pilose to villose, rarely glandular, thickening in fruit. **Calyx** 8–22 mm long, 3–8 mm in diameter, tubular to tubular-campanulate, with variable yellow to yellowish brown pubescence, sparsely to densely villous, rarely pilose or glandular, light green to purple, firmly membranaceous, teeth 1–5 mm long, erect, sometimes recurved in fruit, triangular to ovate, acute at apex; calyx in fruit campanulate to urceolate, becoming coriaceous, striate-nerved. **Corolla** tube 17–25 mm long, 1–3 mm in diameter, 1–2 times as long as calyx, sparsely pilose or glabrous, pale violet below, white toward apex, limb 18–32 mm in diameter, plane spreading, lobes subequal, broadly rounded to truncate at apex, lateral margins. **Stamens** included in upper part of tube; filaments slender, slightly broader at base, glabrous, white, lower pair 2–4 mm long, upper pair 4–5 mm long; anthers 1 mm long, oblong-reniform. **Ovary** 1–5 mm long, ovoid-conical, green; style 17–18 mm long, filiform, bright green; stigma 1–2 mm long, briefly bifid, the upper lobe somewhat larger, bright green. **Capsule** 8–13 mm long, 8–10 mm in diameter, enclosed by calyx, ovoid to subglobose, apically apiculate, smooth, shiny, light to dark green, pericarp thin, 0.5 mm thick, cartilaginous to crustaceous, dry at maturity, sparingly dehiscent. **Seeds** (2)7–10, 4–6 mm long, 3 mm in diameter, oblong-ovoid, more or less angular, dark reddish brown, reticulate-pitted. **Embryo** 4 mm long, very slightly curved; cotyledons 1.5 mm long, ovate-elliptic.

DISTRIBUTION—Brazil. See Figure 23.

Key to the Subspecies of *Brunfelsia brasiliensis* (Spreng.) L. B. Sm. & Downs

1. Inflorescence terminal, nearly sessile, compact, with 1–8 flowers; peduncles shorter than pedicels; pedicels 5–15 mm long; calyx 15–22 mm long; leaves often glabrescent . . . . . **10a.** subsp. *macrocalyx*
1. Inflorescence terminal and subterminal, lax or dense, often branched, with 8–many flowers; peduncles equaling or longer than pedicels; pedicels 2–5 mm long; calyx 7–17 mm long; leaves usually pubescent-villous beneath . . . . . **10b.** subsp. *brasiliensis*

10a. *Brunfelsia brasiliensis* subsp. *brasiliensis*. Figure 24.

Franciscea acuminata Pohl, Pl. Bras. Icon. Descr. 1: 4, t. 3. 1826. Type: BRAZIL. Rio de Janeiro: in umbrosis inter frutices ad Mandioca, *Schott 6163* (holotype, BR).

Brunfelsia acuminata (Pohl) Benth. in DC., Prodr. 10: 199. 1846.

Brunfelsia brasiliensis var. *acuminata* (Pohl) L. B. Sm. & Downs in Reitz, Fl. Ilustr. Catar., pt. 1, Sola: 305. 1966.

Franciscea ramosissima Pohl, Pl. Bras. Icon. Descr. 1: 5, t. 4. 1826. Type: BRAZIL. Rio de Janeiro: ad Serra Tingua, *Schott 3720* (holotype, W; isotypes, GH, W).

Brunfelsia ramosissima (Pohl) Benth. in DC., Prodr., 10: 199. 1846.

Franciscea confertiflora Pohl, Pl. Bras. Icon. Descr. 1: 6, t. 5. 1826. Type: BRAZIL. Minas Gerais: inter frutices locis umbrosis in via de Villa Fanado vel Bom Successo dicta ad Villa do Principe, Oct.–Nov. 1820, *Pohl 3478* (holotype, W; isotype, W).

Brunfelsia confertiflora (Pohl) Benth. in DC., Prodr., 10: 199. 1846.

Brunfelsia ramosissima var. *confertiflora* (Pohl) J. A. Schmidt in Mart., Fl. Bras. 8(1): 260. 1864.

Franciscea divaricata Pohl, Pl. Bras. Icon. Descr. 1: 6, t. 6. 1826. Type: BRAZIL. Minas Gerais: inter frutices, locis umbrosis in via de São João d'El Rey, ad Villa Paracatudo Principe, floret ab Octubri usque ad Martium, 1818, *Pohl 593, 6165* (holotype, W; isotypes, F, GH LE, W).

Brunfelsia ramosissima var. *laxiflora* J. A. Schmidt in Mart., Fl. Bras. 8(1):260. 1864. Type: BRAZIL. Brasilia meridionalis, without locality, *Sellow s.n.* (holotype, M).

Brunfelsia ramosissima var. *parcifolia* J. A. Schmidt in Mart., Fl. Bras. 8(1):260. 1864. Type: BRAZIL. Minas Gerais: without locality, *Claussen 171* (holotype, BR).

FIG. 23. Distribution of *Brunfelsia brasiliensis* (solid square) and *B. chiricaspi* (solid circle).

Leaves 3–13 cm long, 1–4.5 cm wide, puberulent or scabrous above, often glabrescent, variably villous beneath, often densely so at midrib, firmly membranaceous to subcoriaceous. **Inflorescence** variable, dense to lax, occasionally elongate and well-developed, with 10–many flowers, rarely reduced to about 5. **Peduncles** equaling or longer than pedicels, 2–10 mm long, rufo-villous, not glandular. **Pedicels** 2–5 mm long, villous. **Calyx** 7–15 mm long, variably villous with dense, yellowish brown hairs, rarely pilose or glabrescent, eglandular. **Corolla** tube 17–22 mm long, 1.5–2 times as long as calyx; limb 16–30 mm in diameter.

DISTRIBUTION—Brazil (Distrito Federal, Goiás, Minas Gerais, Paraná, Rio de Janeiro, São Paulo).

SPECIMENS EXAMINED—**BRAZIL. Distrito Federal:** gallery forest ca. 10 km NW of Planaltina, 950 m, 27 Feb. 1966, *Irwin et al. 13194* (US); gallery forest ca. 10 km E of Lagoa Paranoa, near DF-6, 1000 m, 25 Feb. 1970, *Irwin et al. 26556* (WIS); *Brasilia; Bacia do Rio São Bartolomeu, Corrego Forquilha, *Heringer et al. 6148* (F). **Goiás:** *25 km NW of Brasilia, *Irwin et al. 15799* (F). **Minas Gerais:** Mun. Santo Luzia, Fazenda da Chicaca, 1100 m, 20 Nov. 1945, *Assis 102* (GH, R, US), *Assis 137* (GH), *Assis 142* (GH), 13 Dec. 1945, *Assis 181* (GH, UC, US); Lagoa Santa, Oct.–Nov. 1863, *Engler 1006* (C), 14 Jan. 1864, *Engler 1009* (C), 30 Oct. 1863, *Engler sp. nov.* (C), 25 Mar. 1933, *Mello Barreto 7786* (F), *Warming 103* (NY, S); Serra do Cipo, km 120, 2 Sep. 1933, *Mello Barreto 7788*; Mun. Belo Horizonte, Morro do Candido, Jan. 1934, *Atamp. 6560* (R); Matta da Caixa d'Areia, 15 Dec. 1918, *Gehrt 3276* (SP);

FIG. 24. *Brunfelsia brasiliensis* subsp. *brasiliensis* (originally as *Franciscea confertiflora*). From Pohl, J. E., *Plantarum Brasiliae Icones et Descriptiones* (1826).

estrada para Lagoa Santa, 15 Jan. 1951, *Joly 1133* (SP); Villa Paraiso, 20 Nov. 1922, *Mello Barreto 7789* (F); Barreiro, 21 Jan. 1933, *Mello Barreto 7791* (F); Serra do Taquaril, 18 Jan. 1933, *Mello Barreto 7791* (F), 29 Mar. 1933, *Mello Barreto 7793* (F); Jardim Botânico, 17 Nov. 1933, *Mello Barreto 7794* (R); Serra da Mutuca, 27 Jan. 1945, *Moreira 5775* (GH); Fazenda da Baleia, 4 Mar. 1940, *Oliveira 21* (US); Morro das Pedras, 3 km S of Belo Horizonte, 1000 m, 12 Feb. 1945, *Williams & Assis* (GH); near Lagoa Pampulha, 1000 m, 8 Mar. 1945, *Williams & Assis 6088* (F, GH, MO, NY); Mun. Carandai, Carandai, km 416, 25 Nov. 1946, *Duarte 631* (GH, RB); Hermilo Alves, 10 Jan. 1965, *Duarte 8741* (GH, RB); Mun. Ouro Preto, Itacolomi, 1400 m, 31 Dec. 1950, *Macedo 2829* (MO, NY, S); Mun. Araxa, Barreiro, 10 Feb. 1951, *Macedo 3131* (S, SP, US); Mun. Santa Barbara, Serra do Caraça, 14 Apr. 1933, *Mello Barreto 7784* (F); Mun. Tombos, Fazenda das Antilhas, 21 Jan. 1936, *Mello Barreto 7767* (F, R); Mun. Diamantina, Serra dos Crystais, 6 Nov. 1937, *Mello Barreto 9603* (F, R); Po de Araca, 17 Nov. 1937, *Mello Barreto 9833* (F, R); Mun. Jaboticatubas, Lagoa de Dona Ignacia, 6 Jan. 1940, *Mello Barreto 10530* (R); Mun. Viçosa, state agricultural school, 17 Dec. 1958, *Irwin 2269* (NY, R, US); Fazenda de Dr. Christioma, 700 m, 30 Dec. 1930, *Mexia 5467* (BM, BH, F, G, GH, MICH, MO, NY, PH, S, UC); Mun. Serro, 3 km from Serro, 12 May 1945, *Williams & Assis 6859* (GH); Aguas Virtuosas, 15 Jan. 1919, *A. Amaral s.n.* (SP); Soçego, Jan. 1921, *A. Amaral s.n.* (SP); Carmo do Rio Calro, Fazenda Corrego Bonito, 5 Sep. 1961, *Andrade 1024, Emmerich 985* (US); Campanha, Nov. 1896, *Brandão 2066* (R); Serra do Cipo, km 131–132, Palacio, 4 Dec. 1949, *Duarte 2029* (GH, RB); Arraial do Pinheiro, Oct. 1840, *G. Gardner 5063* (BM, CGE, F, G, GH, K, NY, P, US, W); Serra do Palmital, 24 Jun. 1884, *Glaziou 15311* (C, K, R); Santa Barbara do Mato Dentro, 12 Jan. 1921, *Hoehne 4920* (SP, US); Caeti, Nov. 1915, *Hoehne 6129* (R); Sabara, Jan. 1916, *Hoehne 6846* (US); Serra de Grão Mogol, 1,100 m, 12 Nov. 1938, *Markgraf 3495* (RB); prope Pitangui, Cueillie a Sabana, 11 Mar. 1862, *Netto s.n.* (R); Barbacena, 21–24 Jun. 1879, *Netto et al. s.n.* (R); BR-4, km 938, 40 km depois de Medina, 16 Jan. 1965, *Pabst 8340, Pereira 9451* (HB, RB); Serra do Cipo (Conceição), 1,200 m, 22 Dec. 1948, *Palacios, Balegno & Cuezzo 3467* (B, W); Caldas, 3 Feb. 1857, *Regnell I-375* (BR, C, M, P, R, S, US); Itabura, 1816–1821, *St. Hilaire D-80* (MO, NY); Penha, *St. Hilaire s.n.* (US); Sítio, 20 Nov. 1905, *Sampaio 68, 74* (R, US); Serra de Itabira do Campo, 11 Sep. 1887, *Schwacke s.n.* (R, US), 20 Dec. 1888, *Schwacke s.n.* (R); Congonhas do Campos, 1843, *Stephan s.n.* (BR); Serra do Frio, 1833, *Vauthier 541* (GH, K, L, W); Serra da Mantiqueira, Passa Quatra, Estação Florestal da Mantiqueira, 31 Jun. 1949, *Vidal s.n.* (R); without locality, *Capanema s.n.* (GH, RB), 1842–1843, *Claussen 146* (BM, CGE), *Claussen 147* (BM, CGE), *Claussen 157* (W), 1840, *Claussen 334* (BR), *Claussen s.n.* (BM, BR, GH, K, W), *Weddell 1648* (P); *Serra do Espinhaço, SW of Rio Jequiti and Mendanha on road to Diamantina, *Anderson 8949* (F, MO); *Municipio Tombas; Fazenda das Antilhas, *Mello Barreto 7787* (F, R); *Belo Horizonte; Serra do Taquaril, Hab. Canga, *Barreto 7790* (F); *ca. 17 km SW of Minas Gerais–Bahia state border, *Davidse et al. 11611* (MO); *13 km W of Lavras along Highway 265 to Barbacena, *Davidse & Ramamoorthy 10709A* (F); *Municipio Pato de Minas; Corrego Barreiras, *Hatschbach 42939* (F); *Municipio Itamonte; Serra da Mantiqueira, *Hatschbach & Kummrow 45569* (F); *Municipio Diamantina; Biri-Biri, *Hatschbach & Pelanda 27993* (GH); *Serra do Espinhaço, Serra do Itabirito ca. 45 km S of Belo Horizonte, *Irwin et al. 19549* (MO); *Serra do Espinhaço, Serra do Cipo, *Irwin et al. 20150* (MO); *Serra do Espinhaço, *Irwin et al. 29189* (MO); *Serra de Espinhaço, S of Ouro Preto, *Irwin et al. 29407* (MO); *Serra do Espinhaço, ca 34 km E of Belo Horizonte, *Irwin et al. 30628* (MO); *Municipio Lima Duarte; Conceicão do Ibitipoca, Parque Florestal Estadual de Ibitipoca, *Souza et al. 521* (F). **Paraná:** *Municipio Senges, Rio Cajuru, *Hatschbach 43398* (F); *Ponte Nova–Minas Gerais, *Hatschbach & Ahumada 31333* (MBM). **Rio de Janeiro:** Monte Corcovado, 300–700 m, 6 Mar. 1924, *L.H. & E.Z. Bailey 758* (BH); by way of Laranjeiras, 31 Dec. 1825, *Burchell 1372* (P), 1841, *Claussen s.n.* (W), 26 Dec. 1920, *Ducke & J.G. Kuhlmann s.n.* (RB); summit, 1836, *Gardner 248* (BM, CGE, G, K, W), 10 Jan. 1865, *Glaziou 812* (BR, C, R), May 1838, *Guillemin 825* (P), *Langsdorff s.n.* (US), Nov.–Dec. 1832, *Luschnath s.n.* (BR), 1834, *Luschnath s.n.* (BR), 700 m, 22 May 1969, *Plowman 2786, Sucre 5086*, (GH, ECON, PH, RB), Feb. 1832, *Riedel 467* (L, GOET, LE), Nov.–Dec. 1832, *Riedel 1190* (L, LE), 12 Jul. 1915, *Rose & Russel 20221* (GH, US); Pico da Tijuca, 18 Jan. 1931, *Brade 10569* (R), *Brade 10583* (GH, R), 1838, *Guillemin 41* (P); Excelsior, 3 Feb. 1930, *J.G. Kuhlmann s.n.* (GH, RB), Dec. 1824, *Riedel 1249* (LE), 23 Aug. 1896, *Ule s.n.* (R); mata da Tijuca, 10 Nov. 1896, *Ule s.n.* (R), 1836, *Vauthier*

42 (F, G, P). Novo Friburgo, 9 Dec. 1918, *Curran 619* (GH, S, SP), *Curran 623* (F, GH); Morro Possole, Sítio Dr. Dungs, 1300 m, 28 Jan. 1968, *Pabst 9115* (HB), 23 Dec. 1887, *Glaziou 17170* (BR, C, LE, P, US); Petropolis, 1883, *Glaziou 14171* (BR, C, G); prés de la roche de Juraracacu, 25 Mar. 1879, *Glaziou 11394* (C, P); Carangola, Sep. 1943, *Goes & Constantino 543* (RB); Retiro, Nov. 1943, *Goes & Constantino 710* (RB); Caetetu, Dec. 1943, *Goes & Constantino 883* (RB); Estrada de Contorno, 650 m, 2 Feb. 1968, *Sucre 2360*, *Braga 203* (GH, RB); Mata do Judeo, 700 m, 7 Dec. 1968, *Sucre 4213*, *Braga 1169* (RB), 1858–1860, *Wawra & Maly 426* (LE, W); Terexopolis, Parque Nacional da Serra dos Orgãos, 16 Dec. 1942, *Duarte de Barros 1195* (RB); Posso, Morro das Antenas de Televisão, 12 Feb. 1968, *Sucre 2339*, *Braga 182* (GH, RB); Serra dos Orgãos, 3000 ft, 7 Jan. 1837, *Gardner 564* (BM, CGE, G, GH, K, NY, US, W), 1885, *Glaziou 15132* (C, G, K, LE), May 1839, *Guillemin 954* (P); Imbuhy Lane, Jan. 1838, *Miers 4495* (US), 900 m, Dec. 1952, *Vidal II-5784* (R); Santa Ana, 1822–1823, *Beyrich s.n.* (P, S); Montagnes prés Sumidoro, *Laland s.n.* (P); Cantagallo, *Peckolt 181* (W); ad confines Rio de Janeiro–Minas Gerais, in graminosis partis superioris montis Itatiaia, 2000–2500 m, Sep. 1901, *Wettstein & Schiffner s.n.* (W); without locality, 1834, *Gaudichaud 442* (G, P), *Raben 703* (BR), 1840, *Regnell 173* (S), 1832, *Riedel s.n.* (GH, GOET, L, LE, NY, P, S, US, W), *St. Hilaire A-746* (P), 1838–1842, *U.S. South Pacific Exploring Expedition s.n.* (NY), Oct. 1916, *Vincent s.n.* (L), *Widgren 486* (S); *Morro Queimado, *Almeida 1286* (F); *Floresta da Tijuca; Pedra do Archer, *Angeli 250* (F); *Morro Queimado, *Brade 18785* (F); *Rio de Janeiro, Pedra da Gavea, base da Chamine, *Carauta 2420* (F); *Guanabara; Pedra da Gavea, Mesa, *Carauta and de Oliveira 1523* (F); *Guanabara; Tijuca, *Castellanos 23973* (F); *Municipio de Macaé, Pico de Frade, *Farney et al. 584* (F); *Municipio de Macaé, Pico de Frade, *Farney et al. 597* (F, RB); *Rio de Janeiro; Alto de Boa Vista, Estrada da Vista Chinesa, mata atras do Decam, *Landrum et al. 4150* (F); *Tijuca, Bom Retiro, *Pabst 7411* (F); *Estrada da Vista Chinesa, *Strang 172* (F); *Pedra da Gavea, *Sucre 7446* (F); *Morro Queimado, *Sucre 8002* (F); *Serra da Carioca, no topo do Morro Queimado, *Vianna et al. 1574* (F). **São Paulo:** Jundiahy, region of Morro da Mursa, 1000 m, 4 Apr. 1915, *Brade 7020* (SP); São Paulo, Vila Ema, Dec. 1932, *Brade 12119* (R), Jan. 1952, *Brade 21218* (RB); Campos do Jordão, 10 Sep. 1937, *Campos Porto 3381* (R), *Campos Porto s.n.* (GH, RB), 22 Oct. 1938, *Hashimoto 1* (RB), 27 Jul. 1898, *Löfgren 3986* (SP); Atibaia, Nov. 1931, *Constantino s.n.* (RB); Guaratingueta, 27 Jan. 1920, *Gehrt 3667* (SP); Mogi das Cruzes, 18 Apr. 1921, *Hoehne 5481* (SP, US), Oct. 1833, *Riedel 1466* (G, LE, NY, US); São José dos Campos, 17 Dec. 1908, *Löfgren 86* (RB, S); ca. 7.7 km SW em linha reta da praça principal de São José dos Campos, 300 m, NW da Via Dutra, 600 m, 25 Oct. 1961, *Mimura 53* (US); Ipiranga, Dec. 1912, *Luderwaldt 1086* (RB, SP), Jun. 1907, *Usteri 23/306* (NY); Taubate, *Lund 754*, *Lund 756* (C); inter Lorena et Taubate, Apr. 1833, *Riedel 1465* (K, LE, NY); Serra da Bocaina, Jan. 1925, *Lutz s.n.* (R); in nemorosis editis retro Bananal in via publica versus São Paulo, Dec. 1817, *Martius s.n.* (M); Morro Formozo, Dec. 1817, *Martius s.n.* (M); Serra da Mantíqueira, Fazenda de Cruzeiro do Dr. Major Novaes, 3–12 Jan. 1884, *Saldanha 8587* (R); *Municipio São Jose de Barreiro; Parque Nacional da Serra da Bocaine, Fazenda das Garrafas, *Lima, H.C. de, & Ramamoorthy 1224* (F); *Municipio Registro; Rod. Registro–Sete Barras, *Hatschbach & Guimarães 45004* (F); *Serra da Bocaina, *W. Hoehne 6154* (F), **W. Hoehne 6155* (F); *Salesopolis; Estação Biologica de Boracea, perto do Rio Coruja, *Mattos, J., & Mattos, N., 14284* (F); *Serra da Bocaina; Parque Nacional, *Occhioni 9174* (F). **Without state:** *Bowie & Cunningham 228* (BM, S), 1842, *Dupré s.n.* (BR, NY, P), *Germain 171* (F), *Guillemin 171* (G), *Lobb s.n.* (K), *Martius 1292* (G, L, M, NY), *Pohl 263* (PR), *265* (PR), *266* (PR), *Schüch s.n.* (BR, W), *Sellow s.n.* (BM, BR, CGE, F, K, L, M, S), *Weir 23* (CGE, K).

10b. *Brunfelsia brasiliensis* subsp. *macrocalyx* (Dusén) Plowman *comb. et stat. nov.*

Brunfelsia hopeana var. *macrocalyx* Dusén, Archiv. Mus. Nac. Rio de Janeiro 13: 94. 1905. Type: BRAZIL, Rio de Janeiro, na mata da encosta da Serra do Itatiaia, in silva, 1600 m, 5 Jan. 1896, *Ule 636* (holotype, R 66551).

Leaves 3–8 cm long, 1.2–2.2 cm wide, glabrous and often nitid above, glabrescent beneath or with pubescent midrib and nerves, subcoriaceous to coriaceous. **Inflorescence** short, subsessile, terminal, with 2–8 flowers, rarely reduced to 1. **Peduncles** 2–5 mm long, usually much shorter than pedicel, sparsely long-pilose or densely glandular-pubescent. **Pedicel** 5–15 mm long, villous or glandular-pubescent. **Calyx** 15–22 mm long, pilose or glandular-pubescent or glabrescent. **Corolla** tube 18–25 mm long, scarcely exserted from

calyx or up to 1½ times as long; limb 25–32 mm in diameter.

DISTRIBUTION—Brazil (Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina, São Paulo).

SPECIMENS EXAMINED—**BRAZIL. Minas Gerais:** Mun. Diamantina, Guinda, 5 Nov. 1937, *Mello Barreto 9479* (F, R). **Paraná:** Ipiranga, Monte Alegre, 1100 m, *Dusén 3388* (R); Bauhado, 13 Dec. 1911, *Dusén 13562* (GH, NY, S); Guaratuba, 21 Feb. 1952, *Reitz 4375* (US); *Palmeira, *Hatschbach 11878* (MBM); *Barra Rio Papagaios (Balsa Nova), *Hatschbach 18747* (MBM); *Municipio Guaratuba; Rio Sai, *Hatschbach 19447* (MBM); *Municipio Jaquariaiva; Fazenda Chapada S. Antonio, *Hatschbach 20997* (GH); *Municipio Pirquara; Serra do Emboque, *Hatschbach 26532* (MBM); *Municipio Pirai do Sul; Joaquim Murtinho, *Hatschbach 39209* (GH, MBM); *Municipio Palmeira, Rio Tibagi, *Kummrow 970* (GH); *Brandalize, *Lindeman and Haas 1174* (U). **Rio de Janeiro:** Alto Macahé de Nova Friburgo, 22 Jan. 1874, *Glaziou 6908* (BR, C, S), *Glaziou 13478* (C, F, LE); 1882, *Glaziou 14172* (C, G, LE); Petropolis a Itamaraty, 25 Mar. 1879, *Glaziou 11395* (BR, C, G, LE, R); Serra dos Orgãos, 18 Nov. 1887, *Glaziou 17169* (BR, C, P, R), 2,200 m, Jun. 1915, *Lützelburg 6187* (M); Morro Assu, 2400 m, Jan. 1916, *Lützelburg 6559* (M, NY), Feb. 1838, *Miers s.n.* (BM); Serra do Itatiaia: 1900 m, Sep. 1913, *Brade & Tamandare 6576* (SP), 1915, *Campos Porto 173* (R, RB), 2100 m, Jun. 1902, *Dusén 569* (R), 18 Oct. 1903, *Dusén 2023* (K, R, S, US), 1750 m, 28 Oct. 1927, *Ginzberger 93* (F), *Moreira s.n.* (R); Parque Nacional de Itatiaia, km 15, 17 Aug. 1948, *Occhioni 1131* (GH, RB); prope Registro, 1800 m, 14 Nov. 1954, *Pabst & Brade 10283* (US); Macieras, 1900 m, Sep. 1934, *Brade 14074* (B, R, RB), 1800–2000 m, 23 Oct. 1927, *Zerny s.n.* (W); entre Maromba e Macieiras, 1820 m, 29 May 1969, *Plowman 2891, Sucre 5191* (ECON, GH, MICH, PH, RB, UC, VEN), 1,700 m, *Plowman 2906, Sucre 5206* (GH, MICH, PH, RB), 1200–1900 m, 22°27′S, 44°39′W, 10 Jan. 1929, *L.B. Smith 1788* (GH, S, US), 26 Feb. 1965, *Vogel 677* (US); *Parque Nacional de Itatiaia, *Lindeman & Haas 5157* (U); *Parque Naçional de Itatiaia; entre Maromba e Macieras, *Sucre 5806* (F). **Santa Catarina:** Mun. Salete, Taio, Ribeiro Grande, 16 Dec. 1950, *Reitz 3985* (G, NY, UC, US); Mun. Rio do Sul, Alto Matador, 800 m, *Reitz & Klein 7601* (US). **São Paulo:** Alto da Serra, 2 Feb. 1913, *Brade 6037* (S, SP), *Brade 7625* (US), 2 Dec. 1920, *Hoehne 4595* (SP, US), 22 Dec. 1919, *Hoehne 8250* (SP, US), 27 Nov. 1902, *Puttemans 5890* (SP); Serra da Bocaina, 1650 m, 12 May 1951, *Brade 20953* (RB); Fazenda Campo Grande, Linha Ferrea Ingleza, 17 Nov. 1892, *Edwall 1981 p.p.* (B, US); Estação Biologica, 800–900 m, lat. 23°46′S, long. 46°20′W, 23 Feb. 1929, *Smith 1989* (GH, US); Campos do Jordão, Umuarama, 1,750 m, 22 Nov. 1949, *M. Kuhlmann 2338* (SP), 22 Nov. 1957, *M. Kuhlmann 4309* (SP); próximo do Rio Guaratuba, 18 Mar. 1958, *M. Kuhlmann 4359* (SP).

A name that has been in the synonymy of this species, *Gerardia brasiliensis* Spreng., was first published in 1825. Although it was not mentioned by Pohl, both Bentham and Schmidt placed it in synonymy with *B. ramosissima*. This specific epithet was only recently recognized by Smith and Downs (1966) as the first legitimate name and basionym for the species, which now must be called *B. brasiliensis* (Spreng.) L. B. Sm. & Downs.

Sprengel described *G. brasiliensis* from a specimen collected by Sellow in Brazil, and his description, albeit brief, more or less agrees with the present concept of the species. There is, however, one point of difference in Sprengel's description, where he writes "pedunculis axillaribus solitariis." Usually this species has terminal, branched inflorescences, although there may be subterminal axes produced in the uppermost leaf axils.

Unfortunately, Sprengel's herbarium was dismantled and sold after his death by his son. Some of the specimens survived and were eventually deposited at the Berlin herbarium, where they were destroyed in the Second World War (Stafleu, 1967; Stafleu & Cowan, 1985). Sellow apparently made several collections of this species with numerous duplicates, none of which bears collection numbers or localities. It is thus impossible to determine which specimens might be isotypes of the original specimen that Sprengel described. As a representative collection, I selected another specimen of Sellow that was sent to Munich from Berlin in exchange [this is not to be taken as neotypification of the name (see footnote 11)—*Eds.*].

In 1826 Pohl published seven new species of his new genus *Franciscea*, including *F. ramosissima*, *F. acuminata*, *F. confertiflora*, and *F. divaricata*. He stated at that time that these "species" were all closely related but believed that their differences were great enough for them to be considered separate entities. Pohl's specific concepts were generally followed by Bentham, who in 1846 transferred all of Pohl's species of

Franciscea to the genus *Brunfelsia*, omitting only *F. divaricata*, which he placed in synonymy with *B. confertiflora*. According to Bentham, *B. confertiflora* differed from *B. ramosissima* in having a many-flowered, crowded inflorescence, an inflated calyx, and the corolla tube only 1½ times as long as the calyx.

Brunfelsia acuminata as maintained by Bentham was merely a glabrous form of *B. ramosissima*. The type specimen from which Pohl's original drawing was made is preserved in Brussels (BR). A specimen at Vienna (W), collected and apparently annotated by Schott as *F. acuminata*, has a well-developed indument and does not conform to the description of this species. As mentioned above in the discussion of *B. martiana*, there has been considerable confusion of collection data and numbers in the Brazilian collections of Pohl and Schott. For example, the same collection in different herbaria may bear the same number or numbers with either or both names. For this reason the numbers of these two collectors should be used with some caution.

Schmidt (1864), in his account of *Brunfelsia* for *Flora Brasiliensis*, treated this group of "species" as a single variable species, *B. ramosissima*, with three varieties. Variety *laxiflora* included *B. ramosissima* and *B. acuminata* of Bentham, and variety *confertiflora* conformed more or less with his *B. confertiflora*. Schmidt described a third variety, *parcifolia*, for a form with small, coriaceous leaves. Annotations in Schmidt's handwriting on the type and other specimens read "parvifolia," indicating either a typographical error in publication or that he changed his mind. The former is more likely since these plants have quite small, but not few, leaves. This form is now considered only a minor variant.

Brunfelsia brasiliensis is here treated as a single polymorphic species, widely distributed in southern Brazil, with one subspecies, *macrocalyx*, occurring at higher elevations from the Serra do Mar and Serra da Mantiqueira southward in the mountains to Santa Catarina. *Brunfelsia brasiliensis* exhibits a wide range of morphological variation throughout its area of distribution, which consists mostly of mountainous, ecologically diversified terrain. In this region, primarily in the states of Minas Gerais, Rio de Janeiro, and São Paulo, there exist ample opportunities for geographical and ecological isolation of populations with subsequent morphological differentiation.

Environmental factors also play an important part in the phenotypic variability seen in this species, and different forms may be interpreted as ecotypes. For example, in exposed, well-drained places such as the crest of a peak or rocky outcrop, the plants are frequently low in stature with horizontal branches, small, often coriaceous leaves, and fewer and smaller flowers. Lower down the same slope, in shaded, more protected, and probably more fertile places, the plants may attain a height of up to 3 m with well-developed inflorescences and larger flowers and leaves.

The great morphological variation in *B. brasiliensis* occurs chiefly in the presence, type, and location of indumentum, in the size and form of the inflorescence, and to a lesser extent in the size and form of the flowers and leaves.

An important diagnostic feature of this species is the presence of a persistent peduncle, a short stalk that articulates with the pedicel of each flower. This structure is scarcely, if ever, developed in any other species of *Brunfelsia*. Some populations of *B. uniflora*, however, may have a similar stalk in its solitary flowers. This "peduncle" is perhaps more accurately described as an ultimate branch of the inflorescence that immediately precedes a flower. It commonly bears 1–3 small bracts near the base, the axillary buds of which may produce additional flowers, thereby proliferating the inflorescence. The peduncle may be shorter or longer than the pedicel or, more rarely, obsolete. The distal end is dilated into a short, flat torus that becomes conspicuous when the flower falls.

The inflorescence arises at the tips of the branchlets and is usually much-branched and many-flowered. It may be strictly terminal and compact to lax and open with several subterminal branches also developing into flowering axes. Alternatively, the flowers may be reduced to a few, often subsessile ones and rarely to a single flower in subspecies *macrocalyx*. The calyx in *B. brasiliensis* may be tubular to nearly campanulate in form and varies greatly in size. The corolla tube may be scarcely exserted from, or up to twice as long as, the calyx.

The presence of a well-developed indument, particularly in the inflorescence, is also diagnostic in *B. brasiliensis*. The trichomes are nonglandular, uniseriate, long or short, and straight or curved. In dried material, they are frequently yellowish or yellowish brown. Often the indument may be densely villous to tomentose. More rarely it appears quite sparse and pilose, or the plants may be glabrescent. The upper surface of the leaves is frequently glabrescent, with short, subscabrous hairs that break off near the base. The lower sur-

face of the leaves is usually pubescent, especially at the nerves and midrib.

Brunfelsia brasiliensis is easily distinguished from most other species of the genus by the regularly oblong-lanceolate leaves, the distinctive yellowish brown pubescence, and the presence of the short peduncle articulating with the pedicel. Rare glabrous forms of *B. brasiliensis* (= *B. acuminata* (Pohl) Benth.) resemble *B. bonodora* but are distinguished by their stalked pedicels. *Brunfelsia brasiliensis* appears to be most closely related to the *B. bonodora–B. grandiflora* complex by the nature of the more or less branched inflorescence and floral and fruit morphology.

Brunfelsia brasiliensis subsp. *brasiliensis* is distributed in southeastern Brazil from Minas Gerais south to São Paulo, between 700 and 1400 m elevation. The species shows a fairly wide ecological tolerance but prefers well-drained sites. It is frequently encountered in the *mares de morros*, "the seas of hills," which occur in southeastern Brazil, particularly in Minas Gerais. Here the plant grows on granitic peaks and rocky outcrops, often in dry, exposed habitats. It seems to occur less commonly in the humid forests on the slopes of the Serra do Mar. It also grows in association with the *campos*, or open grassland communities, and in *capães*, small patches of woodland found scattered in the campos. *Brunfelsia brasiliensis* is also encountered in *capoeiras*, a general term for cut-over, secondary woods, and is one of the few brunfelsias that survive cutting of the primary forests. Around Brasilia, it has been reported from gallery forests. *Brunfelsia brasiliensis* is a freely flowering plant with the flowers appearing primarily from September to March. The fruits have been collected from October to March. This species has been cultivated in European conservatories since its discovery, although it is much rarer in cultivation than other species. To my knowledge, it is not planted in the American tropics outside of Brazil. Peckolt (1909) says that it is a common garden plant in that country. *Brunfelsia brasiliensis* is known as *manacá*, *manacá da serra*, *erva de macaco*, and *manacá assu* (Peckolt, 1909). From herbarium labels (*Occhioni s.n.*, *V. Assis 102*, *142*) we know that it is considered poisonous.

At higher elevations in the mountains of Rio de Janeiro, São Paulo, and south to Santa Catarina, there occurs a distinct subspecies of *B. brasiliensis*. This was first described by Dusén in 1905 as *B. hopeana* var. *macrocalyx* from a specimen collected on Mount Itatiaia. This type superficially resembles *B. uniflora* (=*B. hopeana*) in having the inflorescence reduced to a single flower, but this is somewhat exceptional for the subspecies as now circumscribed.

Brunfelsia brasiliensis subsp. *macrocalyx* differs from *B. brasiliensis* subsp. *brasiliensis* in having fewer flowers per inflorescence (one to eight), a very short peduncle in which the flowers may appear sessile, a longer pedicel (5–15 mm) that always exceeds the peduncle, and a usually longer calyx (15–22 mm). The corolla tube of subspecies *macrocalyx* is short relative to the calyx and is just barely exserted. The indumentum is frequently less well-developed, especially in the leaves, which may be glabrescent and bright green. In addition, the trichomes may be glandular, especially in the calyx and pedicels, a character not normally encountered in subspecies *brasiliensis*.

Morphologically intermediate populations are known to exist between subspecies *brasiliensis* and subspecies *macrocalyx*. In collections from the Serra dos Orgãos and Alto Macahé in the state of Rio de Janeiro, subspecies *brasiliensis* shows a tendency to develop a large calyx (to 17 mm) similar to that of subspecies *macrocalyx*. However, because these plants are, in general, larger in all parts, they may be considered exceptionally vigorous individuals perhaps growing in a particularly favorable place (cf. *Glaziou 6908*, *13478*, *17169*). Other collections (cf. *Occhioni 1131*) from Mount Itatiaia are referable to subspecies *macrocalyx*, although they exhibit a multiflorous inflorescence. These plants may indeed suggest putative hybridization between the two subspecies; however, this cannot be proved at this stage of knowledge of the group. Several collections from the states of Paraná and Santa Catarina have been referred to *B. brasiliensis* subsp. *macrocalyx* (e.g., *Dusen 13562*, *Reitz 3985*). These populations are somewhat heterogeneous and in some characters resemble *B. cuneifolia* (see discussion under that species), such as the indument and the reduction in number of flowers, often to one. Furthermore, the calyx tends to be smaller than in more northern populations of this subspecies, somewhat resembling that of subspecies *brasiliensis*.

Because of the complex pattern of variation that is encountered in this region, I believe this problem cannot be resolved completely without additional materials and a knowledge of the plants in the field.

Brunfelsia brasiliensis subsp. *macrocalyx* in the

northern part of its range occurs at altitudes between 1650 and 2400 m on relatively few mountain peaks and high campos: Mount Itatiaia, Alto Macahé, and Serra dos Orgãos in Rio de Janeiro; and Alto da Serra, Serra de Bocaina, and Campos do Jordão in Sãão Paulo. In São Paulo (Campo Grande) and southward, subspecies *macrocalyx* occurs at somewhat lower elevations (800–900 m).

Ecologically, it grows in wet, montane cloud forests in association with *Podocarpus* and also occurs in moist, high-elevation campos. In the Parque Nacional de Itatiaia, plants have been frequently collected between Maromba and Macieiras at 1600–1900 m elevation and are represented by two distinct forms. One of these (cf. *Plowman 2891*, *Sucre 5191*) is sparsely branched with dark leaves and pubescent calyx with erect lobes. The other (cf. *Plowman 2906*, *Sucre 5206*), which grows sympatrically a few hundred yards away, is profusely branched with bright green, glabrous leaves and a glabrous calyx with strongly recurved lobes. Though strikingly different to the casual observer, these plants must be regarded as minor phenotypic variants of a single subspecies. Analysis in the field of situations such as this gives a measure of the kind of variability that is present in a population and a better basis for understanding comparable problems where field studies are not possible.

Efforts were made to rear these plants in the greenhouse from seed to study the nature of the characters and their inheritance. However, the seedlings proved to be exceedingly sensitive to fluctuations in temperature and humidity and soon died.

11. ***Brunfelsia chiricaspi*** Plowman, Bot. Mus. Leafl. 23(6): 255, t. 17. 1973. Type: COLOMBIA. Putumayo: Umbria, 0°54′N, 76°10′W, 325 m, forest, shrub 1.5 m, flowers sky blue, *zanango*, medicinal, Oct.–Nov. 1930, *Klug 1810* (holotype, A; isotypes, F, S, US 1456539). **Figure 25.**

Shrub or treelet 1–3 m tall. **Trunk** to 5 cm in diameter near base. **Bark** thin, roughish, grayish brown. **Branches** few, lax, spreading, naked. **Branchlets** glabrous, light brown to ochraceous, shiny, outer bark thin. **Leaves** scattered along branchlets or somewhat crowded, blade 20–30 cm long, 7–12 cm wide, elliptic to lanceolate, sometimes obovate, apically obtuse with short, subfalcate acumen or acuminate, cuneate to blunt at base, glabrous, dull, dark green above, pale green beneath, smooth, subcoriaceous, lateral nerves 8–10, straight; petiole 5–10 mm long, short, stout, glabrous, dark brown, roughish. **Inflorescence** corymbiform, terminal or axillary, usually few-flowered with 4–7(20) flowers, puberulent or glabrous. **Bracts** 1–2 mm long, lanceolate, concave, glabrous. **Flowers** sky blue to violet, fading white, with 5-angled white spot at mouth. **Pedicels** 6–13 mm long, slender, glabrous. **Calyx** 10–13 mm long, 4–6 mm in diameter, tubular-campanulate, slightly inflated, glabrous, purplish to pale green, teeth short, broadly triangular, acute to blunt with short glandular acumen; calyx in fruit coriaceous, striately nerved, dotted with lenticels. **Corolla** tube 22–25 mm long, 3 mm in diameter, twice as long as calyx, straight, glabrous; limb 25–30 mm across, thickening at mouth prominent, fleshy, 5-angled, lobes subequal, strongly deflexed at anthesis, the uppermost slightly larger, rounded. **Stamens** included in upper part of corolla tube; filaments subligulate, lower inner pair 2.5 mm long, upper outer pair 3.5 mm long, reaching the mouth; anthers to 1.5 mm long, orbicular-reniform, light brown. **Ovary** 2 mm long, ovoid-conical; style filamentous, equaling filaments; stigma briefly bifid, obtuse, the upper lobe somewhat larger. **Capsule** about 10 mm long, 8 mm in diameter, dry at maturity, subglobose. **Seeds** few, 6 mm long, 2.5 mm in diameter, ellipsoid-reniform, reticulate-pitted.

DISTRIBUTION—Colombia, Ecuador. See Figure 23.

SPECIMENS EXAMINED—**COLOMBIA. Putumayo:** Orito, near Texaco drilling site, 11 Feb. 1972, *Kennedy 1386* (GH); alrededores de Puerto Limón, 300–400 m, 15 Feb. 1953, *Mora 1040* (COL); El Whiskey at Finca "Santa Marta," 13 km S. of Umbria near road, 400–500 m, 27 Nov. 1968, *Plowman 2080* (ECON, GH); forest about 2 km SW of San Pedro, N of Puerto Asis, 400–500 m, 28 Nov. 1968, *Plowman 2081* (ECON, GH); Río Guamues, San Antonio, 5 Sep. 1966, *Pinkley 420* (ECON); Santa Rosa, 28 Nov. 1966, *Pinkley 563* (ECON); trail between Santa Rosa and road to Hormiga, 2 Dec. 1968, *Plowman 2092* (ECON, GH); *Río Putumayo, Puerto Ospina, *Schultes 3422* (GH). **ECUADOR. Napo:** *Along Río Aguarico upstream from Santa Cecilia, *Duke 16047* (MO); *Coca (Puerto Francisco de Orellana), S side of Río Napo, *Harling & Andersson 11771* (GB); *Coca (Puerto Francisco de Orellana), *Harling & Andersson 11804* (GB, GH); *Hacienda Cotapino

FIG. 25. *Brunfelsia chiricaspi*. Reproduced courtesy of the Botanical Museum of Harvard University.

(Concepción), *Harling et al. 7021* (GB, GH); *Path Cotapino (Concepción), Río Bueno, *Harling et al. 7151* (GB, GH); *Coca de Orellana, lower Río Payamino, *Harling et al. 7772* (GB, GH); *Hacienda San Carlos at Río Napo, ca. 15 km E of Coca (Puerto Francisco de Orellana), *Lugo 2724* (GB, GH); *Tierra Colorada, ca. 3 km N of Coca (Puerto Francisco de Orellana), *Lugo 2942* (GB, GH); *Cañon de los Monos, road Coca (Puerto Francisco de Orellana), Lago Agrio, ca. 12 km N of Coca,

Lugo 2981 (GB, GH); *road from Lago Agrio–E 1 Chaco, *Lugo 3476* (GB, GH); *7 km N of Coca; Estacion Experimental de INIAP–Payamino, *Zaruma et al. 56* (F).

Brunfelsia chiricaspi was originally known only from a few collections from a small area of southwestern Colombia on the eastern flank of the Cordillera Occidental. [Plowman predicted that the distribution would prove to be much greater, and this species is now also known from many recent collections in adjacent Ecuador (see above).—*Eds.*] It grows as an understory shrub in humid, primary forests at elevations of 325–500 m. The fruit is as yet imperfectly known because of a lack of material.

Brunfelsia chiricaspi is related to *B. grandiflora*, which is widespread in the western Amazon, and to *B. mire* of Bolivia and adjacent Peru and Brazil. *Brunfelsia chiricaspi* differs from *B. grandiflora* in having larger leaves, longer pedicels (6–13 vs. 2–6 mm) and usually fewer flowers. It differs from *B. mire* in the basally obtuse, elliptic to lanceolate leaves; the few-flowered cyme; and smaller flowers (corolla tube 22–25 vs. 25–38 mm long).

Known generally as *chiricaspi* in the Colombian Putumayo, this species is used as a strong medicine and narcotic by the Kofán Indians (see Plowman, 1977).

12. *Brunfelsia cuneifolia* J. A. Schmidt in Mart., Fl. Bras. 8(1): 259. 1864. Type: BRAZIL. In Brasilia australiore, *Sellow 4016* (lectotype, designated here, destroyed at Berlin; photograph of lectotype, F 621824, NY, US; isolectotypes, F, M).[13] *Riedel 1467*, also cited by Schmidt, is excluded as a type. It belongs to *B. obovata* Benth. var. *obovata*. **Figure 26.**

Shrub to about 1 m tall, much branched. **Branches** terete, naked. **Bark** grayish to yellowish brown. **Branchlets** short, leafy, sparsely to densely villous, rarely glabrescent, hairs often yellowish to reddish brown, sometimes glandular. **Leaves** scattered or crowded near the tips of the branchlets, blade 3.5–10 cm long, 1.8–3 cm wide, oblong-obovate to elliptic-lanceolate, cuneate to blunt at apex, rarely acuminate, narrowed to broadly cuneate at base, the upper surface glabrescent or with long, scattered hairs, the lower surface velutinous, often densely so at midrib and nerves, rarely glandular or glabrescent, somewhat shiny above, dark green, pale green beneath, firmly membranaceous to subcoriaceous, lateral nerves 4–7; petiole 2–4 mm long, velutinous or glandular. **Inflorescence** terminal on tip of branchlets, sessile, with 1–3 flowers. **Bracts** 2–8 mm long, small, lanceolate, glandular, ciliolate, caducous. **Flowers** violet fading to white with age. **Pedicel** 3–5 mm long, slender, thickened at apex, velutinous or glandular pubescent. **Calyx** 12–18 mm long, 4–6 mm in diameter, tubular, inflated, 5-angled, drying plicate, pubescent with short glandular hairs, especially near base, or villous, pale green, membranaceous, teeth 3–7 mm long, ovate-lanceolate, acute to acuminate at apex. **Corolla** tube 18–28 mm long, 1.5–2 mm in diameter, 1½ times as long as calyx, pentagonal at base, pilose or minutely glandular in upper part; limb 25–37 mm in diameter, spreading, lobes 10–15 mm long, undulate, broadly rounded. **Stamens** inserted in upper part of tube; upper pair of filaments 3–4 mm long, suberect, exserted slightly from mouth; lower pair 2–3 mm long, included, curved at apex; anthers 1.5 mm long, orbicular-reniform. **Ovary** 2 mm long, conical-ovoid, style about 23 mm long, filamentous; stigma 1 mm long, briefly bifid. **Fruit** and **seed** unknown.

DISTRIBUTION—Brazil (Paraná, Rio Grande do Sul, Santa Catarina, São Paulo). See Figure 28.

SPECIMENS EXAMINED—**BRAZIL. Paraná:** Mun. Mangeirinha, Lageado San Antonio, 20 Oct. 1966, *Hatschbach 15159* (US); *Municipio de Guarapuara; Guarapuara, *Frenzel 666* (MBM); *Inacio Martins, *Hatschbach & Guimarães 30302* (MBM); *Municipio Campo Largo; Serra do Puruna, *Kummrow 2432* (F). **Rio Grande do Sul:** Farroupilha, 15 Oct. 1957, *Camargo 2123* (B), 3 Oct. 1957, *Camargo s.n.* (S); *Municipio Cacequi, *Dobereiner & Tokarnia 732* (RB); *Esmeralda; Estacion Ecologica de Aracuri, *Jarenkow 132* (F). **Santa Catarina:** Mun. Lajes, Passo do Socorro,

[13] It is clear that Plowman was intending to lectotypify this species using the destroyed B sheet as good photographs of it exist. He appears to specifically not consider the unnumbered Sellow sheets at F and M as good candidates for lectotypes (in the strict sense).—*Eds.*

→

FIG. 26. *Brunfelsia cuneifolia.*

PREFEITURA MUNICIPAL DE CURITIBA
MUSEU BOTÂNICO MUNICIPAL

HERBÁRIO Nº

FAM. Solanaceae

N.V.

N.C. Brunfelsia cuneifolia J. A. Schmidt

LOC. Águas Sta. Clara (mun. Guarapuava) Paraná

LEG. G. Hatschbach 50573 2/10/1986

DET. T. Plowman 1988.

OBS. Arbusto 2 m; flor lilas. Interior mata de galeria.

PMC - DPP 004

Nº 1995963

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OF
NATURAL HISTORY

900 m, 31 Oct. 1963, *Klein 4343* (US); Mun. Novo Horizonte, Lauro Müller, 400 m, 24 Oct. 1958, *Reitz & Klein 4076* (NY, US); Campos Novos, 12 Sep. 1963, *Reitz & Klein 16158* (GH, US); Mun. Campos Alegre, lower fazenda of Ernesto Scheide, Campo Alegre, 900 m, 11 Dec. 1956, *Smith & Klein 8567* (US); Mun. Chapeco, Guatambu, ca. 27°06′S, 52°45′W, 350–400 m, *Smith & Reitz 12541* (GH, R, NY, US); Mun. Irani, Campo de Irani, ca. 26°57′S, 51°50′W, 700–900 m, 8 Nov. 1964, *Smith & Klein 13044* (GH, MO, P, R, UC, US). **São Paulo:** Ilha do Cardoso, perto de Cananeia, *Prance et al. 6933* (F).

In his original description of *B. cuneifolia* in Martius's *Flora Brasiliensis* (1864), Schmidt cited two syntypes. One of these, *Riedel 1467*, is clearly *B. obovata* of Bentham. The other, which now serves as the type, was collected by Sellow in southern Brazil, but no specific locality was given. The specimen cited by Schmidt (*Sellow 4016*) was destroyed at the Berlin herbarium; two unnumbered Sellow duplicates, at Chicago (F) and Munich (M), which conform in every way with the photograph of the type, may be considered isolectotypes.

Known from only a few collections, the available material of *B. cuneifolia* shows a considerable amount of variation in the form of the leaves and type and amount of indument. *Brunfelsia cuneifolia* is distinguished from other species of southern Brazil by the apically cuneate leaves and a five-angled tubular calyx that appears plicate when pressed and dried. The leaves and calyces are always pubescent with either of two types of trichomes present. The type collection and material from Rio Grande do Sul have short glandular hairs. Most specimens from Santa Catarina have a dense villous to velutinous indument consisting of longer, nonglandular hairs. The form of the leaves and calyx associated with both types is fairly uniform.

Brunfelsia cuneifolia is not easily distinguished from other species of southernmost Brazil. It superficially resembles *B. pilosa*, which is sympatric with *B. cuneifolia*. *Brunfelsia pilosa*, however, usually has a more pronounced acumen in the leaf and a terete, tubular calyx that is purple and bears only a few, long pilose hairs. In addition, the flowers of *B. pilosa* are somewhat larger than those of *B. cuneifolia*.

The villous pubescence of *B. cuneifolia* is very reminiscent of the yellowish indument characteristic of *B. brasiliensis*. Populations interpreted here as *B. brasiliensis* subsp. *macrocalyx* extend as far south as Santa Catarina and overlap with the range of *B. cuneifolia*. Collections of these two species in this region are morphologically very similar and may be easily confused. *Brunfelsia brasiliensis* subsp. *macrocalyx* may be separated by the presence of the persistent peduncle, which articulates with the pedicel of the flowers, and by the terete, campanulate or tubular-campanulate calyces. This species usually has longer pedicels and shorter calyx teeth than *B. cuneifolia*. Nevertheless, the intermediate nature of these populations indicates that some hybridization may have occurred between these two species and possibly involved *B. pilosa* as well.

The true affinities of *B. cuneifolia* appear to lie with *B. obovata* var. *obovata*, which occurs farther north in São Paulo and Minas Gerais [but see also *B. boliviana.—Eds.*]. This plant resembles *B. cuneifolia* in the tubular pentagonal calyx, which also nearly equals the corolla tube in length, and in the obovate leaves. In both species the uppermost pair of anthers may be briefly exserted from the corolla tube, a character that is unusual in section *Franciscea*. *Brunfelsia cuneifolia* differs in having the leaves cuneate at the apex, fewer flowers per inflorescence, and a pubescent calyx that is much more slender than in *B. obovata* (4–6 vs. 6–10 mm). These two species also differ strikingly in their ecological preference. *Brunfelsia obovata* is a plant of marshes and flooded areas, whereas *B. cuneifolia* occurs in uplands.

Brunfelsia cuneifolia is a relatively low shrub that is found in habitats apparently similar to those of *B. pilosa*. It is specifically reported from *Araucaria* forests (*arau-carieto*) and also from gallery forest and *capoeiras*, or secondary forest, and between 400 and 900 m altitude. It flowers in October and November and is known by the common name *flor de Trovoada*, or "thunderstorm flower."

13. *Brunfelsia dwyeri* D'Arcy, Ann. Missouri Bot. Gard. 57:259. 1971 ("1970"). Type: PANAMÁ. Panamá: Cerro Jefe in "Cleusia"

→

FIG. 27. *Brunfelsia dwyeri*.

Revision of Brunfelsia (Solanaceae)

Brunfelsia dwyeri D'Arcy

Det. by Timothy Plowman I-1974

BOTANICAL MUSEUM
HARVARD UNIVERSITY
CAMBRIDGE, MASS

PLANTS OF PANAMA
COLLECTED FOR THE HERBARIUM OF
DUKE UNIVERSITY

Brunfelsia dwyeri D'Arcy
det. by R.L. Wilbur, 1971.

Provincia de Panamá: slopes of Cerro Jefé beyond Cerro Azul between 4-8 miles in mostly heavily wooded slopes.

Common shrub 2-5 m. tall. Corolla deep violet blue becoming paler with age.

R.L. Wilbur #11358
R.E. Weaver 25 January 1970

1709790

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OF
NATURAL HISTORY

(sic) forest, 2700–3000 ft, shrub, flowers purple to whitish purple, 27 Jan. 1966, *Tyson, Dwyer & Blum 3312* (holotype, MO 1820936; isotype, MO 1917560). *Duke & Dwyer 13933* (MO) is excluded from the cited paratypes. **Figure 27.**

Shrub or small tree 2–10 m tall. **Trunk** to 6–8 cm in diameter, branched from near the base. **Bark** gray to grayish brown. **Branches** terete or somewhat angular, naked. **Branchlets** leafy. **Leaves** with blade 5–11 cm long, 2.5–5 cm wide, obovate, elliptic or oblong-lanceolate, acuminate at apex, slightly revolute at margin, cuneate or narrowed at base, glabrous, shiny and light to very dark green above, pale green beneath, coriaceous, lateral nerves 5–7, veinlets reticulate, prominulous, especially on lower surface; petiole 3–10 mm long, becoming transversely corrugate-rugose. **Flowers** solitary, terminal or axillary in the upper leaf axils, purple, fading to white with age, with irregular white spot at mouth. **Peduncle** 1–5 mm long, sometimes obsolete. **Bracts** 1–3 mm long, linear to ovate, puberulent, ciliate-margined, caducous. **Pedicel** 5–15 mm long, about 2 mm in diameter, glabrous. **Calyx** 12–22 mm long, 5–10 mm in diameter, tubular to tubular-campanulate, inflated or not so, glabrous, subcoriaceous, reticulately veined, yellowish green or purplish, teeth incumbent or erect, triangular to ovate-lanceolate, at apex acute or blunt; calyx in fruit coriaceous, often becoming dotted with lenticels, verrucose near base, splitting completely along one or two sinuses. **Corolla** tube 25–40 mm long, 2–4 mm in diameter, 2–3 times as long as calyx, glabrous; limb 30–80 mm in diameter, spreading, lobes 10–20 mm long, broadly rounded, the upper lobe slightly larger. **Stamens** inserted in upper part of corolla tube; filaments slender, terete, upper pair about 3 mm long, lower pair about 5 mm long; anthers included within corolla tube, 2 mm in diameter, orbicular-reniform. **Ovary** about 2 mm long, conical, ovoid, weakly 4-angled; style filiform; stigma briefly bifid, the lobes subequal, blunt. **Capsule** 1.5–2.5 cm long, 1–1.5 cm in diameter, globose to ovoid, usually 2-celled, at maturity often appearing 4-lobed with 4 prominent cruciform grooves, pericarp to 4 mm thick, tough and leathery, drying hard, surface smooth and green at first, becoming rugulose-verrucose, light brown. **Seeds** 3–15, 8–10 mm long, 3–4 mm in diameter, oblong-ovoid, prismatic, dark reddish brown, reticulate-pitted. **Embryo** straight, cotyledons ovate.

DISTRIBUTION—Panamá, known only from Cerro Jefe, Provincia de Panamá. See Figure 28.

SPECIMENS EXAMINED—**PANAMÁ. Panamá:** Cerro Jefe, beyond Goofy Lake, 16 Nov. 1967, *Correa & Dressler 471* (MO); along main road before turnoff to summit, 6 Jan. 1971, *Croat 13136* (GH, MO); Cerro Jefe, 8 Apr. 1970, *D'Arcy, Dressler & Correa 3948* (MO), *D'Arcy 3959* (MO), 21 Jan. 1967, *Duke 9429* (MO), 2 Apr. 1969, *Dwyer, Durkee & Castillon 5051* (MO), 12 Mar. 1968, *Dwyer 7280* (GH, MO), ca. 2,900 ft, 29 Jul. 1967, *Dwyer & Gauger 7349* (GH, MO); along road from Cerro Jefe to La Eneida (Cerro Azul), *Croat 13072* (GH, MO), 12 Feb. 1971, *Escobar 359* (COL, ECON, GH), 26 Jul. 1969, *Kennedy 316* (ECON), 12 Apr. 1972, *Plowman 3160* (COL, ECON, GH, MICH, UC), 9 Jul. 1966, *Tyson, Dwyer & Blum 4335* (MO), 2300–2700 ft, 19 Jan. 1969, *Tyson 5315* (MO), 25 Jan. 1970, *Wilbur & Weaver 11358* (GH).

Brunfelsia dwyeri was discovered and described during studies on the flora of Panamá. So far as is known, it occurs only on Cerro Jefe in central Panamá between 700 and 1,000 m elevation, an area now famous for its high floristic endemism (Lewis, 1971). The collection *Duke & Dwyer 13933* (det. W. G. D'Arcy, 1973) from Cerro Pilon in Provincia Coclé, which was cited in the original description as *B. dwyeri*, is actually *Schultesianthus megalandrus* (Dunal) Hunz.

The thick-walled fruit and shiny, coriaceous leaves are distinctive features of *B. dwyeri*. It appears to be most closely related to *B. macrocarpa* of coastal Colombia and Ecuador, the flowers of which are similarly large and solitary and which also possesses a thick-walled fruit. The two species are unique in section *Franciscea* in possessing a fleshy pericarp. The resemblance of *B. dwyeri* to *B. lactea* of Puerto Rico, pointed out by D'Arcy (1971), is indeed "superficial" because these species are placed in separate sections of the genus and have no close affinities with one another.

Brunfelsia dwyeri is a beautiful shrub with attractive, shiny foliage and large, showy flowers. It is locally common in the cloud forests on the upper slopes of Cerro Jefe, occurring in secondary woods with seasonal rainfall. This locality and species represent the northernmost extension of *Brunfelsia* sect. *Franciscea*. As pointed out by Lewis (1971), the entire forest of Cerro Jefe and surrounding areas is rapidly being destroyed for raising poultry and cattle. *Brunfelsia dwyeri* and

FIG. 28. Distribution of *Brunfelsia cuneifolia* (solid triangle), *B. dwyeri* (solid circle), and *B. grandiflora* (solid square).

many other endemic species of plants are in grave danger of extinction.

This species flowers and fruits intermittently throughout the year, although I failed to find flowers in mid-April. Local people reported that the bark and roots of this plant are used for a "remedy."

14. *Brunfelsia grandiflora* D. Don, Edinburgh New Philos. J.: 86. Jul. 1829. Type: PERU. San Martín: Uchiza, 1798, *Tafalla s.n.* (holotype, BM; isotype, MA). **Figure 29.**

Franciscea grandiflora (D. Don) Miers, Ann. Mag. Nat. Hist., ser. 2, 5:250. 1850.

Shrub or small tree 1–6(10) m tall. **Trunk** to 7 cm in diameter near base, much branched. **Bark** thin, roughish, light to dark brown. **Branches** slender, ascending or spreading, often subvirgate and arching, leafy, glabrous. **Branchlets** glabrous, rarely pubescent, green. **Leaves** more or less two-ranked, scattered along branchlets, blade 6–23 cm long, 2–8 cm wide, lanceolate to oblong, often arched with ascending laminas, apically long to short acuminate, the acumen subfalcate, cuneate to narrowed at base, glabrous or sparingly pubescent beneath at midrib, dull, dark green above, paler green beneath, rarely glaucescent or nitid, firmly membranaceous to subcoriaceous; petiole 2–6 mm long, glabrous or minutely pubescent, becoming corky, transversely corrugate with age. **Inflorescence** terminal and subterminal, simple or branched, dense or lax, the axis 5–45 mm long. **Flowers** 5–many, showy, scentless, violet fading to white with age, with rounded, white ring at

mouth. **Bracts** 1–3 per flower, 1–5(10) mm long, lanceolate to ovate, ciliolate, pubescent or glabrate, caducous. **Pedicel** 2–5(10) mm long, glabrous or with few sparse glandular hairs, becoming thicker and corky-verrucose in fruit. **Calyx** 5–13 mm long, 3–7 mm in diameter, tubular-campanulate, somewhat narrowed toward base, globose to obovate in bud, somewhat inflated or not so, glabrous, rarely punctate or sparsely glandular within, smooth or striate-nerved, light yellow-green to gray-green, firmly membranaceous to subcoriaceous, teeth 1–5 mm long, triangular to ovate, blunt to short acuminate, erect or incumbent, recurved slightly with age; calyx in fruit persistent, coriaceous, becoming corky-verrucose especially near base, often splitting on one or more sides. **Corolla** tube 15–40 mm long, 1.5–3 mm in diameter, 2–5 times as long as calyx, glabrous, pale violet to white; limb 20–50 mm in diameter, spreading, violet fading to white with age, lobes 7–15 mm long, subequal or uppermost somewhat larger, rounded or emarginate at apex, overlapping at sides, abruptly narrowed at base. **Stamens** completely included in upper part of corolla tube; filaments thin, upper pair 4 mm long, lower pair 3 mm long, white; anthers 1–1.5 mm long, orbicular-reniform, light brown. **Ovary** 1.5–2 mm long, sessile, conical to ovoid, pale yellow; style slender, slightly dilated at apex; stigma about 1 mm long, briefly bifid, unequal, the upper lobe somewhat larger, obtuse, green. **Fruit** 8–20 mm long, 8–20 mm in diameter, ovoid to subglobose, obtuse or apiculate at apex, smooth, nitid, dark green turning brownish, with corky-punctate or -verrucose outgrowths, pericarp thin, 0.3 mm thick, crustaceous, drying brittle, tardily dehiscent. **Seeds** 10–20, 5–7 mm long, 2–3 mm in diameter, variable in shape, ellipsoid to oblong, angular, dark reddish brown, reticulate-pitted. **Embryo** about 4 mm long; slightly curved, cotyledons 1.5 mm long, ovate-elliptic.

DISTRIBUTION—Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia. See Figure 28.

Key to the Subspecies of *Brunfelsia grandiflora*

1. Corolla tube 30–45 mm long, 2–3.5 mm in diameter, opening at mouth linear-oblong; limb 35–42 mm in diameter, capsule 17–22 mm long ..... 14a. subsp. *grandiflora*
1. Corolla tube 15–30 mm long, 1–2 mm in diameter, opening at mouth elliptic-obovate; limb 20–40 mm in diameter; capsule 11–16 mm long ..... 14b. subsp. *schultesii*

14a. *Brunfelsia grandiflora* subsp. *grandiflora*

Brunfelsia calycina f. *grandiflora* (D. Don) Voss in Vilm., Blumengärtner, ed. 3, 1: 743. 1896.
Brunfelsia tastevinii Benoist, Bull. Soc. Bot. France 75: 295. 1928. Type: BRAZIL. Acre: region de Rio Jordão, *Tastevin s.n.* (holotype, P; isotypes, F, P).

Leaves 10–23 cm long, 3–8 cm wide, glabrous or sparingly pubescent at midrib; petiole 3–12 mm long. **Pedicel** 2–10 mm long. **Calyx** 9–13 mm long, teeth 2–5 mm long, ovate-lanceolate. **Corolla** tube 30–45 mm long, 2.5–3.5 mm in diameter, the mouth 6–9 mm long; limb 35–52 mm in diameter, spreading. **Capsule** 17–22 mm long.

DISTRIBUTION—Colombia, Ecuador, Peru, Brazil, Bolivia.

SPECIMENS EXAMINED—**COLOMBIA. Meta:** *25 km S from Granada toward San Juan, *Luteyn et al. 4769* (F, MO). **ECUADOR. Loja:** *City of Loja, *Zarucchi & Andrade 2316* (F). **Napo:** Mera, 4 Mar. 1940, *Lugo 23* (S); Cantón Napo, near Achidona, 650 m, 19 Apr. 1935, *Mexia 7275* (F, S, UC, US); *Costado S del Río Napo, E de Puerto Napo, por carretera nueva hacia Río Arajuno, *Neill 6546* (F); *Río Napo 8 km abajo de Puerto Misahualli; Reserva Biológica Jatun Sacha, *Neill & Palacios 7101* (F). **Zamora-Chinchipe:** Reg. Oriental, Huamboya, 1500–1600 m, 15 Feb. 1944, *Acosta-Solis 7576* (F); Camino Gualaquiza al Río Zamora (Las Jibarias), 850 m, 25 Dec. 1948, *Scolnik 1495* (US); *Zamora–Zumba (along Río Jamboe), *Harling & Andersson 13906* (GB, GH); *Guadalupe–San Jose de Yacuambi (28 de Mayo), along Río Yacuambi, *Harling & Andersson 13934* (GB, GH). **PERU. Cusco.** *Prov. Paucartambo; Callanga, *Woytkowksi 514* (F). **Huánuco:** woods above Pozuzo, 6000 ft, Aug. 1863, *Pearce 290* (K); Monzón, 950 m, 17 Jun. 1958, *Woytkowski 5026* (F, LE, P, S); Divisoria, 1700 m, 16 Sep. 1946, *Woytkowski 34536* (F, MO, UC); *Prov. Tingo Maria; Río Huallaga, *Boeke 1224* (F). **Loreto:** Pongo de Manseriche, Colón, 1924, *Tessmann 5541* (G, S); Río Ucayali, Canchahuayo, 20 Nov. 1898, *Huber 1490* (MG); Santa Catalina, 11 Dec. 1898, *Huber 1562* (MG); Prov. Coronel Portillo, Plantacion Margarita, cerca a la Divisoria, 1500–1600 m, 14 Aug. 1946, *Ferreyra 985* (B, M, US). **San Martín:** Río Huallaga, Río Chipurana, Tarapoto, 6 Dec. 1898, *Huber 1556* (MG);

FIG. 29. *Brunfelsia grandiflora* subsp. *grandiflora* and subsp. *schultesii*. Reproduced courtesy of the Botanical Museum of Harvard University.

*Prov. Mariscal Caceres; Dist. Campanilla, Río Sion, Caserio de Sion, *Schunke, V. 3480* (NY); *Prov. Mariscal Caceres; Dist. Tocache Nuevo, Quebrada de Huaquisha, *Schunke, V. 4051* (NY); *Prov. Mariscal Caceres; Dist. Tocache Nuevo, Quebrada de Huaquisha, *Schunke, V. 4034* (NY). **Without department:** E of the Andes, 4000–6000 ft, Jul. 1884, *Pearce 295* (K); woods near Río Bambusi, one of the tributaries of Marañon, Mar. 1868, *Pearce s.n.* (K); in flum. Marañon ripis inundatis, Apr. 1855, *Spruce 3988* (K); 1909–1914, *Weberbauer 6151* (F). **BRAZIL. Acre:** basin of Rio Purus near mouth of Rio Macauhan (tributary of Rio Yacu), lat. 9°20' S, long. 69°W, 3 Aug. 1933, *Krukoff 5284* (F, G, GH, K, LE, M, MICH, MO, NY, RB, S, SP, UC, US); Rio Moa, 10 km above and below Maita, 16 Apr. 1971, *Prance et al. 11998* (WIS); *Municipio Rio Branco; Rio Branco–Porto Velho Highway, *Albuquerque et al. 1269* (F); *Municipio Rio Branco; Seringal Corredeira, Colocação Terra Alta, *H.C. de Lima et al. 2122* (F); *Cruzeiro do Sul, Rio Jurua and Rio Moa, *Maas et al. 12963* (MO); *Cruzeiro do Sul, *Rosa 622* (MO); *Rio Branco, Rod. Rio Branco–Porto Velho, *J.U. Santos et al. 48* (F). **Amazonas:** Rio Purus, Monte Verde, 18 Apr. 1904, *Huber 4575* (MG), 29 Apr. 1904, *Huber 4589* (MG); Rio Purus–Rio Ituxi, opposite Labrea, 23 Jun. 1971, *Prance et al. 13471* (WIS); Serra da Moa near school, 1 May 1971, *Maas et al. P12709* (WIS); *region of Rio Jordão, *Tastevin s.n.* (F, P). **Without locality:** 1840–1848, *Lobb 65* (K). **BOLIVIA. Beni:** *Tumi Chucua 30 km S of Riberalta along Río Beni, *Solomon 7609* (F); *5 km SW of Riberalta, *Solomon 7905* (F). **La Paz:** *Prov. Nor Yungas: 12 km hacia el Litoral, W del Río Beni, *Beck 13335* (F).

CULTIVATED SPECIMENS OF INTEREST—**ECUADOR. Napo–Pastaza:** Río Aguarico, Dureño, 27 Dec. 1965, *Pinkley 43* (ECON), 24 May 1966, *Pinkley 202* (ECON); Tena, 28 Sep. 1966, *Pinkley 460* (ECON). **PERU. Loreto:** Maynas, Iquitos, 1924, *Tessmann 3541* (G, S). **San Martín:** Monson River, 6 km from Tingo Maria, 625–1100 m, 30 Oct. 1949–19 Feb. 1950, *Allard 21176* (F, US). **BRAZIL. Pará:** Belém, Jardim Botânico do Museu Goeldi, Apr. 1908, BAKER 61 (B, C, G, GH, K, LE, M, NY, US). **Rio de Janeiro:** *Municipio Rio de Janeiro; Jardim Botânico do Rio de Janeiro, *Ferreira & Costa 16* (F).

14b. *Brunfelsia grandiflora* subsp. *schultesii* Plowman, Bot. Mus. Leafl. 23(6):259, t. 18. 1973. Type: COLOMBIA. Amazonas: Río Amazonas, near mouth of Río Loretoyacu and Puerto Nariño, bush 12 ft, flowers white or purple, poisonous to cattle, *sanango*, very positive for alkaloid, 13–15 Sep. 1966, *Schultes, Raffauf & Soejarto 24108* (holotype, GH; isotype, COL).

Leaves 6–20 cm long, 2–8 cm wide, lanceolate, glabrous; petiole 2–6 mm long. **Inflorescence** variable, compact or lax. **Pedicel** 2–6 mm long. **Calyx** 5–10 mm long, teeth 1–3 mm long, triangular to triangular-ovate. **Corolla** tube 15–30 mm long, 1–2 mm in diameter, curved toward apex; limb 20–40 mm in diameter, spreading, mouth 3–5 mm long. **Capsule** 11–16 mm long, 10–16 mm in diameter.

DISTRIBUTION—Colombia, Venezuela, Ecuador, Peru, Bolivia, Brazil.

SPECIMENS EXAMINED—**COLOMBIA. Amazonas:** Leticia, about 1 km NE of town on road to brick factory, 30 Jan. 1969, *Plowman & Kennedy 2310* (ECON); Río Amazonas, forest along river about 2 km downriver from Puerto Nariño near mouth of Río Loretoyacu, 5 Feb. 1969, *Plowman et al. 2404* (GH, INPA, UC); *Río Amazonas, downriver from Puerto Nariño near mouth of Río Loretoyacu, *Plowman et al. 2407* (F). **Caquetá:** Río Orteguaza, La Maria (Hacienda de Ramon Achiardy), 23 km SE of Venecia, 400 m, 7 Mar. 1944, *Hermann 11237* (NY); La Rastra, 22 Apr. 1956, *Vogel 23* (US); Caquetá, Dec. 1930, *Uribe Uribe P. s.n.* (US); Florencia, 420 m, Feb. 1930, *Pérez-Arbelaez 688* (COL, US). **Meta:** llanos of San Martín, 30 Sep. 1916, *Dawe 241* (K, US); San Martín, 400 m, 2 Aug. 1946, *Uribe Uribe 1353* (COL). **Putumayo:** selva higrofila del Río Putumayo, Puerto Porvenir, arriba de Puerto Ospina, hacia la Loma, 230–250 m, 17 Nov. 1940, *Cuatrecasas 10611* (COL); Puerto Ospina, 230 m, 25 Nov. 1940, *Cuatrecasas 10795* (COL, US); Mocoa, bosque higrofilo en la Quebrada del Río Mulato, 570–600 m, 26 Dec. 1940, *Cuatrecasas 11275* (COL, F); camino entre Mocoa y Puerto Asis, 500 m, 21 Jun. 1935, *Garcia Barriga 4586* (COL, US), 500–700 m, 28 Aug. 1963, *Juajibioy Chindoy 277* (ECON); Pepino, 20 Nov. 1968, *Plowman 2039* (ECON), 1800–2400 ft, 16 Mar. 1953, *Schultes & Cabrera 19115* (GH); Río Caqueta, Floresta, about 15 km downriver from Puerto Limón, 20 Dec. 1968, *Plowman 2183* (ECON); Uchupayaco, en la planada entre Urcusique en las orillas del Río Uchupayaco, 300 m, 22 Feb. 1942, *Schultes 3340* (GH); San Antonio del Río Guamues, 7 Sep. 1966,

Pinkley 444 (ECON); along trail between San Antonio and Santa Rosa, 1 Dec. 1968, *Plowman 2090* (ECON). **VENEZUELA. Barinas:** Barinitas, Mar. 1953, *Aristeguieta 1669* (NY, VEN); Parque Barinitas, 600 m, 22 Jun. 1956, *Bernardi 3310* (G). **ECUADOR. Napo:** Rocafuerte, high forest of Hacienda Arcadia, Río Curaray, 200 m, 7 July 1933, *Heinrichs 496* (F, G), Río Aguarico, Dureno, 8 Dec. 1966, *Pinkley 575* (ECON); *confluence of Quiwado and Tiwaneo Rivers, *Davis & Yost 958* (F); *Limoncocha on Río Napo, *Drummond 7330* (MO); *Nuevo Rocafuerte, Río Yasuní, *Harling et al. 7474* (GB, GH); *Río Aguarico, Dureno (30 km E of Santa Cecilia), *Harling et al. 7700* (GB, GH); *Cañon de Los Monos, ca. 12 km N of Coca (Puerto Francisco de Orellana), *Harling & Andersson 11724* (GB); *environs of Limoncocha, *Madison et al. 5390* (F); *Archidona, *Pinkley 457* (F). **Pastaza:** *basin of Río Pastaza, Pacayacu–Sarayacu region, *Gill 45* (NY). **PERU. Cuzco:** Prov. Paucartambo, Villa Carmen, 720 m, 1 May 1965, *Vargas 16301* (US). **Huánuco:** *Prov. Leoncio Prado; Tingo Maria, Castillo, *Plowman 5825* (F); *Prov. Pachitea; Dist. Honoria, Bosque Nacional de Iparia, *Schunke V. 1480* (NY). **Loreto:** Prov. Maynas, Iquitos region, ca. al Cementerio de Iquitos, 120 m, 18 Sep. 1964, *Dodson 2822* (MO); Mishuyacu near Iquitos, 100 m, Jan. 1930, *Klug 741* (US); Rancho Indiana, 110 m, 24 Jan. 1932, *Mexia 6444* (BM, F, G, GH, K, MO, NY, PH, S, UC, US); Río Nanay, upland forest near Samito, 19 Feb. 1969, *Plowman 2494* (ECON, GH); Río Mazan, Gamitanacocha, 100–125 m, 12 Jan. 1935, *Schunke 8* (A, F, NY, UC, US); Masisea, 275 m, *Killip & Smith 26844* (US); Yurimaguas, lower Río Huallaga, 135 m, Aug.–Sep. 1929, *Killip & Smith 27667* (US), *28056* (NY), *28178* (US), Jan. 1831, *Poeppig 2206* (W); Balsapuerto (lower Huallaga Basin), 150–350 m, 28–30 Aug. 1929, *Killip & Smith 28644* (US), 220 m, Feb. 1933, *Klug 2880* (A, F, G, GH, MO, NY, S); Pucallpa, 200 m, 4 Aug. 1946, *Soukup 3041* (F); Pongo de Manseriche, 1924, *Tessmann 4921*, Río Marañon, *Tessman 5005* (G); Prov. Ucayali, lower Pisque, Nueva Beliza, 1923, *Tessmann 3243* (G, NY, S); *Prov. Maynas; Moena Cano between Iquitos and Río Itaya, *Gentry et al. 15707* (MO); *IVITA, km 59 Pucallpa–Tingo Maria road, *Gentry et al. 18573* (MO); *Bosque Nacional von Humboldt, km 86 Pucallpa–Tingo Maria road, *Gentry et al. 18664* (MO); *Prov. Maynas; Negro Urcu, Río Napo, *McDaniel 15328* (MO); *Prov. Maynas; Pebas, mouth of Río Ampiyacu, *Plowman et al. 6455* (F); *Prov. Maynas; Pebas, *Plowman et al. 6737* (F); *Prov. Maynas; Pebas, *Plowman et al. 6939* (F); *Prov. Maynas; Dist. Iquitos, Caserio Momoncillo, *Revilla 304* (MO); *Prov. Maynas; Dist. Iquitos, cerca a la boca del Río Nanay, *Revilla 1724* (MO); *lower Río Nanay, *Williams, Ll., 584* (F). **Madre de Dios:** *ca. 5 km from Puerto Maldonado near Río Tambopata, *Gentry 16249* (MO). **San Martín:** Tarapoto and vicinity, W side of Río Huallaga, S of Shapaja 1–4 km, 900 ft, 28–30 Jul. 1937, *Belshaw 3130* (NY, UC, US); Pucaloma, 330–400 m, 12 Jul. 1950, *Ferreyra 7778* (US), 1855–1856, *Spruce 3973* (BM, BR, CGE, G, MG, NY, W), 350 m, Oct. 1902, *Ule 6481* (G, MG, L), 750 m, Dec. 1929, *Ll. Williams 5482* (F), 830 m, 6 Feb. 1947, *Woytkowski 35008* (F, G, MO, UC); entre Bellavista y Banos 200–300 m, 5 Sep. 1948, *Ferreyra 4760* (US); Zepelacio near Moyobamba, 1100–1200 m, Oct.–Nov. 1933, *Klug 3326* (A, F, G, GH, MO, NY, S); Roque, 19 Jul. 1925, *Melin 186* (S); Saposoa, 400 m, 14 Oct. 1959, *Woytkowski 5525* (F, LE, P, US); Rioja, 800 m, 9 Jan. 1961, *Woytkowski 6170* (GH); Boqueron Pass, 92 km from Tingo Maria on highway to Pucallpa, ca. 400 m, 16 Dec. 1949–5 Jan. 1950, *Allard 22096* (US); *Prov. San Martín; Tarapoto, above Hotel Turista, *Plowman 5984* (F). **Without state:** Peru, 1835, *Matthews 1320* (CGE, K). **BRAZIL. Acre:** Rio Juruá-Mirim, vicinity of Porangaba, 21 May 1971, *Maas et al. P13228* (WIS); Rio Acre, Xapury, Jan. 1911, *Ule 9746* (K, MG); Paraguassu, Seringal, Nov. 1911, *Ule 9749* (K, MG); Rio Branco, 26 Feb. 1962, *Vasconcelos & Coelho s.n.* (INPA). **Amapá:** Rio Oiapoque in shade of virgin forest, 5 km SE of Clevelandia, 3°48′N, 51°53′W, 5 Aug. 1960, *Irwin et al. 47359* (MG, NY); lower slopes and base of Mount Tipac, 0–100 m, 3°36′N, 51°19′W, 16 Oct. 1968, *Irwin 48753* (NY). **Amazonas:** Esperança at mouth of Rio Javary, 26 Jan. 1952, *Ducke 865* (F, GH, MG, MO, R, US); Camatian, 30 Jan. 1949, *Fróes 24035* (RB); Rio Purus, Cachoeira, 21 Mar. 1904, *Huber 4204* (MG); 28 Apr. 1904, *Huber 4377* (MG); Rio Purus, Rio Ituxi, Rio Curuquete, Cachoeira Republica, 24 Jul. 1971, *Prance et al. 14551* (WIS); upper Amazon, in forest near Tabatinga, 30 Nov. 1874, *Traill 599* (K, P); Tocantins, 24 Nov. 1874, *Traill 600* (K, P); Rio Juruá, Bocca do Paranan, Apr. 1901, *Ule 5453* (G, K, MG, L); *Camatian, *Fróes 23974* (GH). **Rondônia:** basin of Rio Madeira, 1 km S of Ribeirão, road Abuna to Guajara–Mirim, 27 Jul. 1968, *Prance et al. 6570* (WIS); *30 km NE de Guajara–Mirim, *Krapovickas & Schinini 35155* (F). **BOLIVIA. Beni:** Río Iboy, Beni, 800 ft, 14 Feb. 1922, *White 2386* (NY, US); Beni River, Jul. 1886, *Rusby 2122* (NY). **La Paz:**

Guanai–Tipuani, Bolivian Plateau, Apr.–Jun. 1892, *Bang 1398* (A, BM, F, G, GH, K, M, MICH, MO, NY, PH, R, US, W); Mapiri, 550 m, 9 Apr. 1927, *Buchtien 1299* (US); Mapiri region, San Carlos at Sarampiuni, 600 m, 28 Feb. 1927, *Buchtien 1300* (US); Charopampa, 570 m, Nov. 1907, *Buchtien 2029* (US), 5,000 ft, Apr. 1886, *Rusby 621* (BM, G, GH, K, LE, MO, NY, PH, US, W); Tumu-pasa, 1800 ft, 7 Jan. 1902, *White 1840* (BM, NY, US). **Pando:** bank of Rio Madeira, 6 km above Abuna, 11 July 1968, *Prance et al. 5854* (WIS); Río Acre, Cobija, Dec. 1911, *Ule 9747* (K, MG), Jan. 1912, *Ule 9748* (G, K, MG). **Santa Cruz:** Prov. Gutierrez, Canton Buenavista, Dolores, 450 m, *Steinbach 1805* (A, UC); Buenavista, 500 m, 14 Dec. 1920, *Steinbach 5487* (GH), 450 m, 2 Jan. 1926, *Steinbach 7399* (A, K); *Buena Vista, Bella Union, *Steinbach 7936* (A, BM, F, K).

Brunfelsia grandiflora was first collected during the Ruiz and Pavón expedition in 1798. Bentham (1846) considered it to be very similar to his *B. latifolia* and perhaps also to its variety. Most material that Bentham referred to *B. latifolia* is now considered *B. grandiflora* subsp. *schultesii*, indicating that he recognized the affinities of the plants concerned, although he misinterpreted *B. latifolia*, which is endemic in Rio de Janeiro (Brazil).

Brunfelsia grandiflora consists of two subspecies: subspecies *grandiflora* and subspecies *schultesii*. Subspecies *grandiflora* is much more limited in its distribution than is the second subspecies. It occurs in the drainage systems of the Ríos Marañon, Huallaga, and Ucayali in Peru; at higher elevations in eastern Ecuador; and in the uppermost tributaries of the Ríos Purus and Juruá in Brazil. It grows primarily at elevations of 650–2000 m in the region known as the *montaña*, humid, montane rain forest that stretches from Colombia to northeasternmost Argentina on the eastern slopes of the Andes.

Brunfelsia grandiflora subsp. *grandiflora* is characterized by its large flowers (to 50 mm across) and fruits (to 22 mm in diameter), as well as by its higher altitudinal preference. Subspecies *schultesii* looks very similar but is generally smaller in all its parts (see key to subspecies). From the relatively few collections available, subspecies *grandiflora* appears to be variable and exhibits some exceptional forms. For example, collections from the northern part of the range (Ecuador and northern Peru) often have divaricating, not spreading, lateral nerves in the leaves and longer pedicels (*Pearce 290*, *Lugo 23*). The latter feature also appears in high-elevation populations of *B. uniflora* in Bolivia.

In the 1920s, a Catholic missionary named Tastevin collected this subspecies in the Rio Tarauaca in the state of Acre, Brazil. He stated that it was a high-climbing liana (Tastevin, 1922) and confused the plant with the psychotropic *Banisteriopsis*. Nevertheless, other collectors have indicated that the plants may reach 10 m in height, an exceptionally large size. Whether *B. grandiflora* subsp. *grandiflora* may actually become lianoid in habit has yet to be confirmed by field observations.

Brunfelsia grandiflora subsp. *grandiflora* is well-known in cultivation, especially in the New World tropics, as an ornamental. In the Amazon region, it is also cultivated for its narcotic and medicinal properties [see Plowman, 1977; Schultes & Raffauf, 1990, 1991—*Eds.*] and is known by several common names: *sanango*, *chici-quisanango*, *chiricsanango*, and *sananguillo* (Peru); and *manacá grande* (Brazil).

Brunfelsia grandiflora subsp. *schultesii* has long been recognized in the literature under several misapplied names, including *B. bonodora*, *B. latifolia*, and *B. maritima*. This was primarily the result of "follow-the-leader" taxonomy in which no botanist consulted the type material on which the original descriptions were based. It is now clear that these other names all apply to species that are found only in southeastern Brazil.

Brunfelsia grandiflora subsp. *schultesii* is wide-ranging and polymorphic, occurring in western South America from Venezuela southward to Bolivia. In addition, disjunct populations are known from the Territory of Amapá in northern Brazil. It grows commonly as an understory shrub in primary and secondary forests between 100 and 900 m elevation. Because this subspecies is widely cultivated in South America for medicinal and ornamental purposes, some activity of man has undoubtedly influenced its present distribution.

The two subspecies of *B. grandiflora* differ primarily in the size and form of the flowers and in the size of the fruits. Subspecies *schultesii* also tends to be smaller in habit and leaf size, but there is considerable overlap between the subspecies in these characters.

The two subspecies are also ecologically and, to some extent, geographically isolated. The typical subspecies is usually found between 900 and 2000 m elevation in the inter-Andean valleys of Peru. *Brunfelsia grandiflora* subsp. *schultesii* nor-

mally occurs at much lower elevations, between 100 and 900 m, throughout the upper Amazon and its tributaries, although isolated populations in Bolivia may reach 1800 m. From morphological and geographical evidence, it appears that subspecies *grandiflora* has arisen from its much more widespread and variable counterpart through isolation in the intermontane valleys.

Intermediates between *B. grandiflora* subsp. *grandiflora* and *B. grandiflora* subsp. *schultesii* are known from areas where the two coexist. This occurs in the Brazilian state of Acre and in the lower Marañon valley of Peru near Pongo de Manseriche (cf. *Tessmann 4921*, *Krukoff 5284*, *Ule 5453*). These specimens are intermediate in the size of their flowers and fruits, which suggests hybridization between the two subspecies in these areas. No intermediate forms have been found in the higher montane valleys or in the tropical lowlands.

As would be expected from such a wide-ranging plant, *B. grandiflora* subsp. *schultesii* shows considerable morphological variation. Some of this variation may be due to environmental factors such as those that exist between the *llanos* of Venezuela and the cloud forests of Bolivia, but it seems that some populations have become genetically differentiated as well since morphologically distinct groups can be readily and consistently separated. These variants, however, are relatively slight and in my judgment should not receive formal names. I will instead discuss some of the more prevalent variations that occur. The most common form of subspecies *schultesii*, represented by the type collection (*Schultes et al. 24108*), is found from the Colombian Putumayo south to Tarapoto in Peru and eastward to Leticia in the Colombian Amazon. These plants have large, more or less oblong-lanceolate leaves and many flowers in a compact inflorescence. It is this form that occurs disjunct in the north Brazilian state of Amapá (*Irwin 47359*, *48753*). This is the only known collection east of Leticia, a disjunction of some 2300 km. The species is apparently absent from the lower Amazon, although additional collecting in this region may prove otherwise.

In the northern part of its range, in the *llanos* of Venezuela and Colombia and south to the Colombian Putumayo, another form of *B. grandiflora* subsp. *schultesii* occurs. These populations have large, oblong, subcoriaceous leaves and more lax, branched inflorescences (cf. *Aristeguieta 1669*, *Pérez-Arbelaez 688*). The leaves in some specimens approach those of *B. chiricaspi* in their large size and ochraceous coloring on drying. These plants apparently survive in scattered patches of woodland in the *llanos* and in gallery forests along the rivers.

A third form of *B. grandiflora* subsp. *schultesii* may be distinguished among populations occurring on the eastern slopes of the Bolivian plateau (cf. *R. S. Williams 425*) in wet, montane forests up to 1600 m altitude. These plants have rather small, lanceolate leaves and few flowers per inflorescence, rarely reduced to three. These populations show strong similarities to *B. bonodora* of the coastal forests of Rio de Janeiro, a species still very poorly known. *Brunfelsia grandiflora* subsp. *schultesii* differs primarily in having shorter pedicels and a smaller calyx, although additional characters may be found when more material becomes available. The floristic affinities between the Yungas regions of Bolivia and Rio de Janeiro have been pointed out elsewhere (Plowman, 1979).

These differing forms of *B. grandiflora* subsp. *schultesii* intergrade completely with adjacent populations and should not be considered taxonomically significant. They are mentioned here to point out the degree of variation that exists in this subspecies, which may, in some cases, lead to confusion with other species.

Brunfelsia grandiflora subsp. *schultesii* grows usually as a shrub 1–2 m tall, at times becoming a treelet to 5–6 m. It lives in the understory of shady, moist forests; at the margins of forest clearings; and along rivers. It commonly persists after the forest has been cut for lumber or shifting agriculture, sprouting easily from the roots. Considered a valuable ornamental and medicinal plant, subspecies *schultesii* is much planted in Indian houseyards and fields and often persists after the inhabitants move elsewhere. In this way, the plant has probably increased its distribution under the influence of man. There is some indication that its occurrence as far east as Leticia in the Colombian Amazon may be due to man's activities. Populations in this area have so far been located only near the major rivers in places most likely inhabited at some time in the past.

Brunfelsia grandiflora subsp. *schultesii* flowers and fruits sporadically throughout the year over most of its range, with two main periods of flowering: December to February and July to August. The flowers are usually unscented, although they may occasionally contain the odor

of jasmine (*Plowman 2019*, *Ducke 865*). This plant is known by a number of vernacular names that are indicative of its usefulness in native medicine [these are given, along with an account of the medicinal and narcotic uses, in Plowman, 1977—*Eds.*].

15. *Brunfelsia hydrangeiformis* (Pohl) Benth. in DC., Prodr., 10: 198. 1846.

Franciscea hydrangeiformis Pohl, Pl. Bras. Ic. 1: 7, t. 7. 1826. Type: BRAZIL. Rio de Janeiro: ad Olaria et Sumido rio in via ad Rio Parahybuna, habitat inter frutices locis umbrosis, floret Septembri et Octubri, 1818, *Pohl (115)* (holotype, W; isotypes, F-875036, M, W).

Shrub 1–2 m tall. **Stem** erect, sparsely branched at intervals. **Bark** grayish brown. **Branches** few, appearing at intervals, 4–6 mm in diameter, stout, naked, glabrous, the epidermis splitting longitudinally. **Leaves** crowded at ends of branches, alternate, subverticellate with 5–10 together, blade 13–32 cm long, 3–15 cm wide, oblanceolate to subspathulate, rarely lanceolate to oblong, abruptly to long acuminate with straight or subfalcate acumen, rarely acute, narrowed-cuneate at base, the upper surface glabrous, often nitid, dark green, the lower surface sparsely pubescent mostly at nerves, or glabrous, pale green, membranaceous to subcoriaceous, reticulately rugose, with sulcate nerves, lateral nerves 7–11, spreading or diverging, depressed in sulci; petiole 2–13 mm long, glabrous. **Inflorescence** terminal, forming in uppermost whorl of leaves, densely capituliform to corymbiform, rarely lax, hemispheric, sessile, the axis 1–3 cm long, persistent. **Flowers** 5–50, purple with white spot at mouth, fading to nearly white with age. **Bracts** paired, 2–10 mm long, lanceolate to linear-lanceolate, pubescent or glabrous, ciliolate at margin. **Pedicel** 2–8 mm long, glabrous or rarely pubescent. **Calyx** 15–35 mm long, 3–10 mm in diameter, tubular to tubular-campanulate, oblong in bud, slightly inflated, variably pubescent, densely pilose, glandular, or glabrous, light green to ferrugineous, thin to firmly membranaceous, teeth 2–10 mm long, erect, ovate to linear-lanceolate, acute to acuminate at apex; calyx in fruit, thin, completely enclosing fruit. **Corolla** tube 20–35(45) mm long, 1–2 mm in diameter, 1–1½ times as long as calyx, rarely longer, slender, glabrous or glandular pubescent; limb 18–32 mm across, spreading, lobes 7–12 mm long, rounded, overlapping at lateral margins. **Stamens** included in upper part of corolla tube; filaments slender, upper pair 5 mm long, lower pair 3 mm long; anthers 1.5–2 mm long, reniform. **Ovary** 2–2.5 mm long, ovoid; style slender, equaling the filaments; stigma briefly bifid, lobes unequal, about 1 mm long. **Fruit** completely enclosed by calyx, 12–20 mm long, 9–15 mm in diameter, ovoid-subglobose, apiculate at apex, smooth, greenish brown, pericarp thin-walled, dry at maturity, crustaceous, sparingly dehiscent. **Seeds** ca. 5–10, 5 mm long, 2 mm in diameter, oblong, irregularly angular, dark brown, deeply reticulate-pitted. **Embryo** unknown.

DISTRIBUTION—Brazil. See Figure 33.

Note: According to the *International Code of Botanical Nomenclature* (Article 60.8, Recommendation 60G) (Greuter et al., 1994), it is recommended that in compound names of Latin origin, the final vowel of the first part be reduced to *i* before a consonant. Thus, correctly, the original orthography of *hydrangeaeformis* is correctable to *hydrangeiformis*.

Key to the Subspecies of *Brunfelsia hydrangeiformis* (Pohl) Benth.

1. Leaves subspathulate to broadly oblanceolate, reticulately rugose with sulcate nerves; pedicel 2–4 mm long; calyx 3–6 mm in diameter with yellowish brown pubescence; calyx teeth 4–10 mm long, linear to linear-lanceolate .... 15a. subsp. *hydrangeiformis*
1. Leaves oblong to oblong-lanceolate, smooth or sulcately nerved; pedicel 4–8 mm long; calyx 5–10 mm in diameter, glabrous or with sparse glandular hairs; calyx teeth 2–4 mm long, ovate to ovate-lanceolate .... 15b. subsp. *capitata*

15a. *Brunfelsia hydrangeiformis* subsp. *hydrangeiformis*. Figure 30 and frontispiece.

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FIG. 30. *Brunfelsia hydrangeiformis* subsp. *hydrangeiformis* (originally as *Franciscea hydrangeiformis*). From Pohl, J. E., Plantarum Brasiliae Icones et Descriptiones (1826).


Franciscea hydrangeaeformis.

Franciscea macrophylla Cham. & Schltdl., Linnaea 2: 601. 1827. Type: BRAZIL. *Sellow sp. nov.* (holotype destroyed at Berlin; fragment of holotype, F-643247; photograph of holotype, F-621825).

Brunfelsia macrophylla (Cham. & Schltdl.) Benth. in DC., Prodr. 10: 198. 1846.

Leaves with blade 18–32 cm long, 6–15 cm wide, subspathulate to broadly oblanceolate, abruptly acuminate, glabrous on both sides, reticulately rugose with sulcate nerves depressed from above. **Pedicel** 2–4 mm long. **Calyx** 18–35 mm long, 3–6 mm in diameter, tubular, scarcely inflated, sparsely pubescent to velutinous with yellowish hairs, otherwise purple to brownish, drying ferrugineous, teeth 4–10 mm long, linear to linear-lanceolate. **Corolla** tube briefly exserted from calyx.

DISTRIBUTION—Brazil (Bahía, Minas Gerais, Rio de Janeiro, São Paulo).

SPECIMENS EXAMINED—**BRAZIL. Bahía:** 1857, *Blanchet s.n.* (G). **Minas Gerais:** Pirange, Oct. 1840, *Gardner 5065* (BM, CGE, F, G, GH, K, NY, P, US, W); São Francisco de Paula, Rio do Peixe, Aug. 1896, *Magalhães 1643* (R); Mun. Serro, Bocada Mata, 1400 m, 6 Oct. 1945, *Williams & Assis 7928* (GH, R, UC, US); Sabara, Nov. 1839, *Claussen s.n.* (BM, BR, G, P); without locality, *Claussen s.n.* (CGE), *Claussen 201* (BR), *Langsdorff s.n.* (US), Sep. 1836, *Raben 14* (C), *Schüch 591* (CGE, W), 1858, *Weddell 878* (G); *km 30–32 on the road from Batinga to Jequitinhonha, *Bunting et al. 10351* (F). **Rio de Janeiro:** Floresta da Tijuca, 7 Aug. 1879, *Glaziou 11393* (K, P), Nov. 1894, *Ule s.n.* (R, US); Serra de Estrella, 1841, *Claussen s.n.* (W); estrada entre a Estrella e a Estrada Rio–Petropolis, 24 Oct. 1932, *J.G. Kuhlmann s.n.* (RB); Nova Friburgo, Oct. 1947, *Leite 4188* (NY); Serra de Friburgo, Sítio do Gaucho, Oct. 1964, *Duarte 8445* (HB); Cachoeira de Macacu, 22 Oct. 1964, *Duarte & Pereira s.n.* (GH, RB); Serra Tingua, Rio San Antonio, 24 Aug. 1879, *Glaziou 11392* (C, NY, P); Rio Parahyba, 1887, *Moura s.n.* (R); Ipiahos, Aug. 1934, *O. Peckolt s.n.* (R); Magdalena, Marreiras, Oct. 1933, *Santos Lima 200* (RB); without locality, *Langsdorff 43* (LE), 1816–1821, *St. Hilaire A-555* (P); *Nova Friburgo, Parada do Gaucho, *Pereira 9241* (F); *Municipio Santa Maria Madalena; Parque do Desengano, Santa Clara, *Araujo 954* (F); *near Mury, *Maas et al. 3326* (U). **São Paulo:** *Municipio de Bananal; Parque Nacional da Serra Bocaina, *Martinelli 1115* (F). **Without state:** 1814–1817, *Bowie & Cunningham 100* (BM), *Sellow s.n.* (F, M, MO, S).

15b. *Brunfelsia hydrangeiformis* subsp. *capitata* (Benth.) Plowman *comb. et stat. nov.* **Figure 31.**

Brunfelsia capitata Benth. in DC., Prodr., 10: 198. 1846. Type: BRAZIL. Rio de Janeiro: Serra dos Orgãos, shrub about 4 ft high growing in rather moist places in virgin forests reaching an elevation of about 4500 ft, *manaca dobrado*, Feb. 1837, *Gardner 563* (holotype, K; isotypes, BM, F 678955, G, NY, P, W).

Franciscea capitata (Benth.) Miers, Ann. Mag. Nat. Hist. Ser. 2, 5:250. 1850.

Brunfelsia capitata var. *angustifolia* Benth. in DC., Prodr., 10:198. 1846. Type: BRAZIL. Rio de Janeiro: Organ Mountains, 1841, *Gardner 5826* (holotype, K).

Brunfelsia hydrangeiformis var. *glabriscula* J. A. Schmidt in Mart., Fl. Bras. 8(1):256. 1864. Lectotype (designated here): BRAZIL. prope Rio, *Gardner 563* (isotypes, BM, F, G, K, NY, P, W). Lectoparatype: BRAZIL. Rio de Janeiro: in montibus prope Nova Friburgo, Jul. 1832, *Riedel 85* (LE).

Leaves with blade 13–26 cm long, 3–11 cm wide, oblong to oblanceolate, rarely lanceolate, acute to acuminate at apex, glabrous on upper surface, puberulent beneath at nerves or glabrous, smooth to sulcately nerved, rarely reticulate rugose. **Pedicel** 4–8 mm long. **Calyx** 14–35 mm long, 5–10 mm in diameter, tubular to tubular-campanulate, often somewhat inflated, glabrous or sparsely glandular pubescent, light green, teeth 2–4(7) mm long, ovate to ovate-lanceolate. **Corolla** tube rarely exserted from calyx.

DISTRIBUTION—Brazil (Espirito Santo, Minas Gerais, Rio de Janeiro, São Paulo).

SPECIMENS EXAMINED—**BRAZIL. Espirito Santo:** Santa Bárbara de Caparão, 4 Dec. 1929. *Mexia 4089-a* (UC, US). **Minas Gerais:** Estaçoão Experimental de Café, Coronel Pacheco, 29 Nov. 1940, *Heringer 460* (RB); without locality, *Ker-*

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FIG. 31. *Brunfelsia hydrangeiformis* subsp. *capitata comb. et stat. nov.* Isotype specimen in the herbarium of The Natural History Museum, London (BM).


Revision of Brunfelsia (Solanaceae)
Brunfelsia hydrangeiformis (Pohl) Benth.
ssp capitata (Benth.) Plowman comb. no
Det. by T. Plowman VII-1976.
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mann 270 (BR), 1824, *Riedel 113* (K, LE), 1816–1821, *St. Hilaire B-58* (P). **Rio de Janeiro:** Pico do Papagaio, Alto da Boa Vista, Oct. 1928, *Brade s.n.* (R), 29 Nov. 1928, *Ducke s.n.* (RB); Nova Friburgo, Nov. 1842, *Claussen s.n.* (F), 6 Dec. 1881, *Glaziou 14173* (C, P); Serra dos Orgãos: Terezopolis, 1888, *Brunet s.n.* (R); Estrada do Fagundes, 9 Dec. 1948, *Duarte & Pereira s.n.* (GH, RB); Parque Nacional da Serra dos Orgãos entre km 8.5–9, 11 Jan. 1960, *Flaster 56* (R); Picada Saudade, 700 m, Jul. 1915, *Lützelburg 6495* (M); Val do Rio Beijaflor, Mato entre Abr. 1 e 2, 1400 m, 30 Dec. 1932, *Markgraf & Apparicio 10495* (RB), *U.S. Exploring Expedition s.n.* (US); caminho para Pedra do Sino, 2000 m, 2 Nov. 1952, *Vidal II-5435* (R, UC). Petropolis, Morin, 20 Jan. 1883, *Glaziou 14174* (C, F, LE, P, R, US); Quitandinha, 790 m, 29 Dec. 1939, *Lutz 1551* (R); Valance, 16 Sep. 1878, *Glaziou 9558* (GH); Cantagallo, 1859, *T. Peckolt 71* (BR); Serra de Estrella, 11 Dec. 1823, *Riedel s.n.* (LE), 1844, *Weddell 818* (NY); Itatiaia, lote 90, 8 Jan. 1947, *Aparicio & Edmundo 868* (RB); Monte Serrat, 2 Jan. 1929, *Campos Porto 1879* (B, RB); without locality, 1838, *Miers s.n.* (F, P), 1844, *Widgren s.n.* (LD, S, US); *Serra dos Orgãos, *Gardner 563* (BM, F, G, K, NY, OXF, P, US, W); *Municipio Santa Maria Madalena; Santa Maria Madalena, Pedra Dubois, *Plowman & de Lima, H.C., 12901* (F). **São Paulo:** Alto da Serra, Jan. 1904, *Edwall 15183* (SP); Serra da Bocaina, *Lutz Boc 14* (R). **Without state:** Caminho de Lucinados, 24 Aug. 1879, *Franklin & Glaziou 5319* (R); *Glaziou 4909* (C), *8471* (C), *Lobb s.n.* (K), Dec. 1837, *Miers s.n.* (NY, US), *Sellow 719* (G), *Sellow s.n.* (BM, F, LE, M), *Widgren 596* (S).

Brunfelsia hydrangeiformis is a beautiful shrub of southeastern Brazil. It grows in moist, shady primary forests between 700 and 2000 m elevation. It is now a rare plant and can be found only in certain protected natural areas, such as the Serra da Estrella and Serra dos Orgãos in the State of Rio de Janeiro and perhaps elsewhere where patches of old forests have survived.

This brunfelsia shows considerable morphological variation, and two subspecies are readily distinguished. The typical subspecies, *hydrangeiformis*, as described by Pohl (Fig. 30) has a long, tubular calyx that is hirsute or rarely glandular pubescent in varying degrees. The leaves of this species are usually broad, often subspathulate, and deeply sulcately veined, giving a rough, reticulate pattern to the surface. The nerves and principal veinlets are sunken in shallow furrows on the upper surface.

A plant related to *B. hydrangeiformis* was described as *Franciscea macrophylla* Cham. and Schltdl. (Chamisso and Schlechtendal, 1827) and later transferred to *B. macrophylla* by Bentham (1846). The type, collected by Sellow, was destroyed in Berlin, but a photograph and fragment are preserved at the Field Museum of Natural History in Chicago. This plant differs from *B. hydrangeiformis* in having a more lax inflorescence in which the pedicels are elongated and articulated with a peduncle, similar to that of *B. brasiliensis*. The entire inflorescence and calyx bear a ferruginous pubescence of sessile glandular hairs, almost scurfy in appearance. Only one modern collection (*Williams & Assis 7928*) from Minas Gerais matches the type of this plant, which appears to be a rare aberrant form of subsp. *hydrangeiformis*.

Brunfelsia hydrangeiformis subsp. *capitata*, originally published by Bentham as *B. capitata*, is a well-defined subspecies differing from subspecies *hydrangeiformis* in having narrower, oblanceolate leaves; longer pedicels (4–8 vs. 2–4 mm); and a glabrous or sparsely pubescent calyx that tends to be tubular-campanulate and broader above than at the middle. In addition, the calyx teeth in subspecies *capitata* are usually ovate instead of linear-lanceolate and shorter (2–4 vs. 4–10 mm). The leaves are often smooth and lack the rugose furrowing of the nerves.

Intermediates between the two subspecies are not uncommon (cf. *Gardner 5065*) and indicate that hybridization probably occurs between them. The subspecies of *B. hydrangeiformis* are not as well-defined, ecologically or geographically, as those in other species of *Brunfelsia*. Subspecies *hydrangeiformis* occurs further inland in Minas Gerais and extends further north than subspecies *capitata*. However, field studies of these plants may reveal ecological differences between them, such as a difference in the time of flowering. Subspecies *hydrangeiformis* flowers from August to November; subspecies *capitata* from October to January, as indicated from herbarium labels.

Brunfelsia hydrangeiformis is most closely related to *B. mire* of Bolivia, a plant that is known from several heterogeneous populations, some of which are very similar to *B. hydrangeiformis*. Their differences are discussed under *B. mire*.

Brunfelsia hydrangeiformis is perhaps the showiest of all the South American brunfelsias and yet has received little attention from horti-

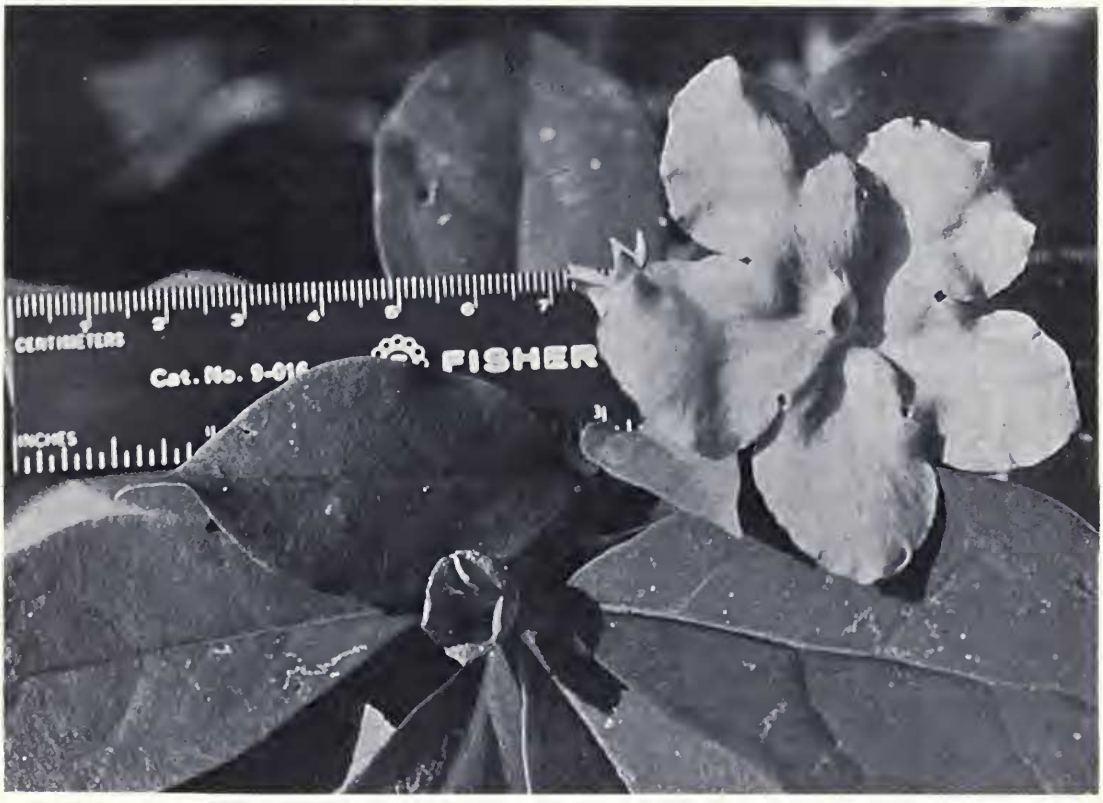

FIG. 32. *Brunfelsia imatacana*. Reproduced courtesy of the Field Museum of Natural History.

culturalists. After a brief period of cultivation in European conservatories, these plants were neglected, possibly because of difficulties in propagation. As indicated by its specific epithet, *B. hydrangeiformis* bears a superficial resemblance to *Hydrangea hortensis*.

16. ***Brunfelsia imatacana*** Plowman, Fieldiana, Bot. n.s. 8: 4, 1981. Type. VENEZUELA. Bolívar: About 20 km NE of Guasipati on road to El Miamo along side road just before Río Cabeza Mala, alt. 200 m, open woodland with white sandy soil. Treelet 4–5 m tall, flowers violet fading pure white with age, odor of jasmine. N. v. *Jazmín del monte*, *Juan de la Calle*. Used for *baños* by healers. 25 Sept. 1968. *T. Plowman 1918* (holotype, F-1813259; isotypes, F-1746565, GH, K, NY, P, UC, US, VEN). **Figure 32.**

Shrub or treelet 3–5 m tall. **Bark** reddish or grayish brown, longitudinally and transversely cracked, shedding in thin flakes. **Branchlets** about 2 mm in diameter, pubescent or glabrate, grayish brown, longitudinally cracked. **Leaves** scattered along branchlets, 65–150 mm long, 20–65 mm wide, oblong-elliptic or elliptic-obovate, short to long acuminate, the apex itself acute to blunt, cuneate to narrowed at base, glabrous or sparsely glandular-pubescent beneath, especially at midrib, dull dark green above, dull paler green beneath, firmly chartaceous to subcoriaceous, the lateral nerves 6–10, spreading, straight to somewhat arching, indistinct; petiole short, 5–10 mm long, 1.5 mm in diameter, pubescent. **Inflorescence** terminal, 1- or 2-flowered, subsessile. **Bracts** 1–3 mm long, linear-lanceolate or squamiform, pubescent, caducous. **Flowers** light violet with a white spot at orifice, fading to pure white with age, fragrant with odor resembling jasmine. **Pedicel** 8–9 mm long, 1 mm in diameter, glabrous, becoming thickened, warty in fruit. **Calyx** 15–21 mm long, 7–10 mm in diameter, tubular, terete, glabrous or with scattered glandular hairs, teeth 4–5 mm long, subequal, ovate, acuminate; calyx in fruit 18–25 mm long, campanulate, thickly coriaceous, dotted

FIG. 33. Distribution of *Brunfelsia hydrangeiformis* (solid triangle), *B. imatacana* (solid square), and *B. mire* (solid circle).

with lenticels. **Corolla** tube 30–38 mm long, 1–2 mm in diameter, twice as long as calyx, straight, with scattered glandular hairs, orifice 3 mm across, lobes 13–23 mm long, subequal, rounded. **Stamens** inserted in upper part of corolla tube; filaments 1 mm wide, strap-shaped; the longer anterior pair 5 mm long, suberect, included in mouth of corolla tube, the shorter posterior pair 3 mm long; anthers orbicular-reniform, upper pair 1.5 mm across, lower pair 1.8 mm across. **Ovary** 1.8 mm long, 2 mm in diameter, broadly ovoid, with 7–8 ovules per locule; style 22–23 mm long; stigma 1.5–2 mm long, briefly bifid. **Capsule** dry at maturity and completely enclosed by coriaceous calyx, 12–17 mm long, 14–16 mm in diameter, ovoid to subglobose, smooth, light green, pericarp 0.5 mm thick, crustaceous. **Seeds** 6–10, 6–9 mm long, 2–5 mm in diameter, oblong-ellipsoid, somewhat angular, reddish brown, reticulate-pitted.

DISTRIBUTION—Restricted to the region of the Serranía de Imataca and Serranía de Núria in the northeastern part of the state of Bolívar, Venezuela. See Figure 33.

SPECIMENS EXAMINED—**VENEZUELA. Bolívar:** Reserva Forestal de Imataca, along logging road to Campamento Paraíso, 28 km NE of Upata, ca. 100 m, 26 Sep. 1968, *Plowman 1919* (ECON, F, GH, K, S, US, VEN); low, flat woodland E of Río Cabeza Mala, 15 km NE of Guasipati, on road to Miamo, 2 Jun. 1960, *Steyermark 86244* (US, VEN); Altiplanicie del Núria, 5 km from Hato de Núria, E of Miamo, 400 m, 10 Jan. 1961, *Steyermark 88290* (NY, VEN); more or less level forest along pica 105, 40 km S of Tumeremo, E of highway

between Tumeremo and El Dorado, 29 km N of El Dorado, 220 m, 23 Jul. 1960, *Steyermark 86574* (NY, US, VEN); Reserva Forestal "La Paragua," márgenes del Río Asa, Jun. 1970, *Blanco 826* (F, VEN); El Dorado, cultivated, Aug. 1957, *Trujillo 3488* (MY).

Previously, I considered *B. imatacana* to be a subspecies of the related species *B. pauciflora* of southeastern Brazil (Plowman, 1973, 1979). Although the two species are superficially similar, *B. imatacana* can be readily distinguished by the leaf shape; the number of lateral nerves; fragrant flowers; the shorter pedicel, calyx, and capsule; and the smaller number and larger size of the seeds. In addition, the two species are widely disjunct by a distance of 3,800 km.

Brunfelsia imatacana is endemic in the northeasternmost part of Bolívar state in Venezuela, in the range of low hills known as the Serranía de Imataca and Serranía de Núria. This area occupies the northern rim of the Venezuelan section of the Guayana Shield. This region has recently been recognized by Steyermark as a distinct phytogeographic unit of the flora of Venezuela. Most of the flora found here represents species of the Guianas at their western limits as well as various eastern Amazonian species at their northeastern limits of dispersal (Steyermark, 1968, 1979). Steyermark (1968) lists 278 plant species known only from the Serranía de Imataca and another 514 species that are restricted to the even more limited area of the Altiplanicie de Núria. The Imataca region has been documented as a major center of both plant and animal species endemism and has been proposed as a Pleistocene forest refuge area (Prance, 1973; Brown, 1979; Steyermark, 1979).

During the collection of the type material, local guides informed me that the foliage of *B. imatacana* was used by healers (*brujos*) for herbal baths. Although this use of the plant was not observed, bulk samples of roots, stems, and leaves were collected for chemical analysis. The freshly air-dried leaves and stems were sent to Dr. John Leary of the Massachusetts College of Pharmacy, Boston, for testing. Dr. Leary (pers. comm., 1973) reported that extracts of this material yielded alkaloid-positive precipitates based on six different precipitating agents. In addition, he obtained a positive test for phytosteroids but negative tests for flavonoids, tannins, and saponins. Dried root, stem, and leaf material of this same sample were also sent to Mr. Jan-Erik Lindgren of the Karolinska Institutet, Stockholm, Sweden. Mr. Lindgren (pers. comm., 1973) prepared methanol extracts of the samples, which were examined by thin-layer chromatography. He also performed a complete alkaloid extraction on the material, followed by gas and thin-layer chromatography on the extracts. Mr. Lindgren was unable to detect the presence of any alkaloids in the samples. It remains uncertain what, if any, active constituents may be present in this species. However, isolation and identification of the active constituents in other brunfelsias with demonstrated pharmacological activity have proved to be similarly difficult (Plowman, 1977; Lloyd et al., 1985).

17. *Brunfelsia latifolia* (Pohl) Benth. in DC., Prodr., 10:199. 1846. **Figure 34.**

Franciscea latifolia Pohl, Pl. Bras. Ic. 1: 3, *t.* 2. 1826. Type: BRAZIL. Rio de Janeiro: Tijuca, habitat in umbrosis, inter frutices, *Schott 6161* (holotype, W).

Brunfelsia maritima Benth. in DC. Prodr., 10: 200. 1846. Type: BRAZIL. Rio de Janeiro: pr. Rio-Janeiro, habitat in maritimis Taipu (holotype, G-DC, non vidi; photograph of holotype, C; isotypes, G-DC, non vidi).

Franciscea maritima (Benth.) Miers, Ann. Mag. Nat. Hist. ser. 2, 5: 250. 1850.

Low **shrub** 0.2–1.0 m tall, much branched from near base. **Branches** often somewhat zigzag, leafy. **Bark** thin, light brown to grayish. **Branchlets** light brown, with internodes about 1 cm long. **Leaves** subsessile, variable in form, blade 4–9 cm long, 2.2–5.5 cm wide, elliptic to oblong, ovate or obovate, apically acute, blunt or rounded, sometimes with a short acumen, or emarginate, basally obtuse to cuneate, rarely truncate, glabrous, at times minutely pubescent beneath at midrib, dull or shiny above, dark green, dull and pale green beneath, firmly membranaceous to coriaceous, lateral nerves 5–8, mostly straight; petiole 1–4 mm long, short, erect, glabrous, dark purple. **Inflorescence** terminal, compact, the axis 3–7 mm long, glabrous. **Flowers** 3–20, pale violet with prominent white thickening at mouth, fading to white, scentless. **Bracts** 1–2 per flower, 1–10 mm long, lanceolate, ciliolate, caducous. **Pedicels** 6–8 mm long, slender, glabrous or sparsely glandular, light green, becoming thicker in fruit. **Calyx** 9–13 mm long, tubular-campanulate, obovoid in bud, glabrous or sparsely glandular, light green, smooth, teeth 2–3 mm long; erect to recurved, triangular to lanceolate, acute at apex, calyx in fruit coriaceous, striately veined, enclosing fruit.


a
B
C
D
E
F
G
H
Franciscea latifolia.

Corolla tube 15–20 mm long, 2 mm in diameter, twice as long as calyx, sparsely glandular, pale violet near base, white toward apex; limb 20–30 mm in diameter, spreading, plane, white beneath, pale violet above fading to white, thickening at mouth rounded or quadrangular, white, lobes slightly unequal, the uppermost smaller, 5 mm long, subtruncate at apex, the others 8 mm long, rounded at apex. **Stamens** included in upper part of corolla tube; filaments slender, cylindric, white, upper pair 2 mm long, lower pair 1 mm long; anthers 1 mm long, orbicular-reniform, brownish. **Ovary** 2 mm long, ovoid, pale green; style slender, white, curved at apex; stigma briefly bifid, lobes unequal, light green. **Capsule** enclosed by persistent calyx, 11–13 mm long, 8–10 mm in diameter, ovoid, apiculate at apex, smooth, glabrous, dark green, pericarp thin-walled, dry at maturity, crustaceous, sparingly dehiscent. **Seeds** 10–12, 5–6 mm long, 3 mm in diameter, oblong-ellipsoid, angular, dark brown, reticulate-pitted. **Embryo** 4 mm long, nearly straight; cotyledons 1.5 mm long, ovate.

DISTRIBUTION—Brazil (Rio de Janeiro). See Figure 37.

SPECIMENS EXAMINED—**BRAZIL. Rio de Janeiro:** Recreio dos Bandeirantes, 22 Oct. 1938, *Alston & Lutz 138* (BM); Pedra de Itauna, BR-6, *J.U. Santos 5790* (US); Jacarepaguá, Pedra de Itauna, 24 Mar. 1971, *Araujo & Kennedy s.n.* (ECON); restinga de Jacarepaguá do lado sudoeste da Pedra de Itauna, 6 Sep. 1969, *Sucre 5314* (GH, RB), 7 Sep. 1969, *Sucre 5348* (GH, RB); Copacabana, Praia Grande, 1834, *Luschnath s.n.* (BR). Lagao de Piratininga, 28 Dec. 1871, *Glaziou 5970* (C); restinga de Piratininga, 8 Nov. 1922, *J.G. Kuhlmann s.n.* (RB); Barra de Marica at the restinga, 7 Nov. 1972, *Rizzini s.n.* (GH); prope Taipu, Apr. 1833, *Riedel 1308* (C, LE); *restinga de Jacarepaguá, Pedra de Itauna, *Sucre et al. 6428* (F), **Vidal 311* (F). **Without state:** *Mikan s.n.* (F, K, W), *Riedel s.n.* (GH).

Brunfelsia latifolia has long been misinterpreted by taxonomists since Bentham's treatment of the genus in 1846. Examination of the type (*Schott 6161*), which is preserved in Vienna, and comparison with contemporary collections make it clear that *B. latifolia* is both morphologically and ecologically distinct from any other species.

Brunfelsia maritima, a species often confused with *B. grandiflora*, is clearly a synonym of *B. latifolia*.

Brunfelsia latifolia is a diminutive shrub endemic to the state of Rio de Janeiro in Brazil, in the environs of the city of Rio de Janeiro. A rare plant, this species grows only in sandy *restingas*, a maritime formation of low shrubs occurring along the sea coast. It flowers from October to April. *Brunfelsia latifolia* is distinguished by its low habit; the rather small, elliptic leaves; and small, pale violet flowers. It seems to be most closely related to *B. bonodora*, an equally rare, erect-growing shrub of the mountains near Rio de Janeiro. This species has narrower, lanceolate leaves and larger flowers than *B. latifolia*. Some specimens (*Mikan s.n.*) are somewhat intermediate between these two species and indicate a close relationship and possibly hybridization. However, this remains to be determined when additional material is available.

In the horticultural trade, the name *B. latifolia* is frequently misapplied to at least two species, *B. australis* and *B. grandiflora*. The confusion between *B. australis* and *B. latifolia* stems from 1841, when Hooker published an illustration of *B. australis* that he misidentified as *B. latifolia*. In reality, *B. latifolia* has never been cultivated as an ornamental.

18. *Brunfelsia macrocarpa* Plowman, Bot. Mus. Leafl. 23(6):251, *t. 16*. 1973. Type: ECUADOR. Esmeraldas: Río Hoja Blanca con Río Hualpi, bosque húmedo primario, 75 m, árbol pequeña del sotobosque, de 7 m, 7 cm d.a.p. Corteza lisa, gris, corola morada, fruto comestible, *guayabilla*, 14 Sep. 1965, *Little & Dixon 21064* (holotype, GH; isotype, US 2639557). **Figure 35.**

Shrub to small tree 2–7 m tall. **Branches** straggling, bare, with smooth grayish bark. **Branchlets** somewhat crooked, terete, glabrous, yellowish brown. **Leaves** sparse toward tips of the branchlets, blade 14–25 cm long, 6.5–11.5 cm wide, broadly elliptic, occasionally oblong, abruptly acuminate at apex, the acumen often subfalcate,

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FIG. 34. *Brunfelsia latifolia* (originally as *Franciscea latifolia*). From Pohl, J. E., Plantarum Brasiliae Icones et Descriptiones (1826).

FIG. 35. *Brunfelsia macrocarpa*. Reproduced courtesy of the Botanical Museum of Harvard University.

blunt or abruptly cuneate at base, glabrous, dark green above, yellowish green beneath, chartaceous, lateral nerves 4–6, spreading; petiole 6–17 mm long, glabrous. **Inflorescence** terminal at tips of branchlets, 1-flowered, bracteate. **Flowers** fragrant, showy, violet turning white with age. **Bracts** few, 2–3 mm long, lanceolate, concave, puberulent. **Pedicel** 8–10 mm long, erect, thickened at apex, glabrous. **Calyx** 20–22 mm long, 6–8 mm in diameter, tubular, ovate in bud, weakly inflated, more or less punctate, firmly membranaceous, teeth 4–8 mm long, subequal, ovate-lanceolate, acute to acuminate at apex; calyx in fruit greatly accrescent, 4–7.5 cm long, to 4 mm thick, coriaceous, somewhat shiny, with punctate lenticels. **Corolla** tube 40–45 mm long, 3–5 mm in diameter, twice as long as calyx, angled in cross section, glabrous; limb 50–55 mm in diameter, spreading, the lobes 18–22 mm long, rounded, subequal, the uppermost a little larger, overlapping at lateral margins. **Stamens** included; filaments subligulate, the upper pair 2 mm long, the lower 3 mm long; anthers 2 mm in diameter, orbicular-reniform. **Ovary** 3 mm long, conical; style 36–38 mm long, slender, curved and thickened at apex; stigma 2 mm long, briefly bifid, gaping, the upper lobe larger. **Fruit** subbaccate, enclosed by accrescent calyx, 4–5 cm long, 4–5 cm in diameter, broadly ovoid or subglobose, smooth, yellow-ochre, pericarp 6–8 mm thick, exocarp leathery, mesocarp thick, fleshy, endocarp thin, cartilaginous, conspicuously veined. **Seeds** 10–20, 10–13 mm long, 5–7 mm in diameter, dark reddish brown, reticulate-pitted. **Embryo** 10–11 mm long, straight; cotyledons 4–5 mm long, broadly ovate.

DISTRIBUTION—Colombia (Nariño), Ecuador (Esmeraldas). See Figure 37.

SPECIMENS EXAMINED—**COLOMBIA. Nariño:** Isla Gorgona, 11–14 Jan. 1837, *Barclay 911* (BM); Costado Oriental, 21 Jun. 1950, *Fernandez 365* (US), 7 Sep. 1924, *Longfield 367* (K).

Known from only a few collections, this interesting treelet occurs in the Island of Gorgona, which lies just off the Pacific coast of southern Colombia, and in the coastal forests of northern Ecuador, where it grows as a small tree in the understory of primary forests. The large, showy flowers are said to be fragrant with the odor of honeysuckle (*Longfield 367*). The fleshy yellow fruit is edible and bears the common name *guayabilla*, or "little guava," which it resembles.

Brunfelsia macrocarpa is a very distinctive species in having a large, fleshy, accrescent calyx that encloses the fleshy yellow fruit. It most closely resembles *B. dwyeri* of Panamá in having large, solitary, purple flowers that fade to white and a thick-walled fruit. However, the fleshy fruit and leaves are also very similar to those of *B. chocoensis*, which is placed in a different section. This resemblance may be due to convergent evolution occurring in these species, which have been isolated for a long period in the lowland Chocó forest under the pressures of a similar and uniform environment. No other species of section *Franciscea* has such a large and fleshy fruit, and *B. macrocarpa* is the only known species of *Brunfelsia* with a large, accrescent calyx.

19. *Brunfelsia mire* Monach., Phytologia 4(5): 342. 1953. Type: BOLIVIA: La Paz: Mapiri Region, San Carlos, 850 m, bäumchen 1 m, blüten violett, 25 Jan. 1927, *Buchtien 1298* (holotype, NY; isotypes K, US 1399371 and 1399372). **Figure 36.**

Shrub 0.2–1.0 m tall, rarely to 2 m, mostly unbranched. **Stem** to 8 mm in diameter, naked, glabrous. **Bark** thin, light to dark brown, rugulose. **Leaves** crowded toward apex of stem, subverticillate, to about 6 per whorl, short petiolate to subsessile, blade 12–28 cm long, 4–8 cm wide, oblanceolate to oblong, rarely ovate-oblong, acute to acuminate, often subfalcate at apex, cuneate to blunt at base, glabrous, dull, dark green above, pale green beneath, subcoriaceous to coriaceous, smooth, lateral nerves 8–13, straight or somewhat arching, spreading, rarely divaricating, veinlets conspicuously reticulate with broad areolae; petiole stout, 2–12 mm long, roughish. **Inflorescence** terminal, arising from upper crown of leaves, sessile, capituliform to corymbiform, usually dense, the axis to 10 mm long. **Flowers** 8–30, showy, violet fading white with age. **Bracts** 2–4 mm long, lanceolate, ciliolate, caducous. **Pedicel** 3–10 mm long, slender, glabrous. **Calyx** 10–18 mm long, 4–8 mm in diameter, tubular to tubular-campanulate, glabrous, rarely sparsely glandular-pubescent, reticulate-veined, teeth 3–7 mm long, ovate to ovate-lanceolate, acuminate; calyx in fruit subcoriaceous, the teeth becoming deeply cut, dotted with lenticels. **Corolla** tube 25–38 mm long, 2–3 mm in diameter, 2–3 times as long as calyx, slender, glabrous or with scattered glandular pubescence; limb 25–50 mm across, spreading, lobes to 15 mm long, broad, rounded, overlapping

FIG. 36. *Brunfelsia mire*. Reproduced courtesy of the Botanical Museum of Harvard University.

at lateral margins. **Stamens** included in upper part of corolla tube; filaments slender, upper pair 4 mm long, lower pair 3 mm long; anthers ca. 1.5 mm long, reniform-hippocrepiform. **Ovary** 2 mm long, ovoid; style filamentous, equaling the filaments; stigma briefly bifid, gaping, lobes ca. 1 mm long, subequal. **Fruit** 13–20 mm long, 12–18 mm in diameter, subglobose to ovoid, apiculate at apex, smooth, pericarp 0.5 mm thick, cartilaginous, dry at maturity, tardily dehiscent. **Seeds** 10–15, 5–6 mm long, 3 mm in diameter, oblong-ellipsoid, angular, dark brown, reticulate-pitted.

DISTRIBUTION—Peru (Cuzco, Puno), Brazil (Acre, Mato Grosso, Pará, Rondônia), Bolivia (Beni, Cochabamba, La Paz, Santa Cruz). See Figure 32.

SPECIMENS EXAMINED—**PERU. Cuzco:** Río Marcopata, 20 km above Quince Mil, 780 m, 15 Jan. 1973, *Madison 986* (GH); Prov. Convención: Echaraté, 900 m, 2 Feb. 1939, *Stork, Horton & Vargas 10461* (G, K, UC); Sahuayaco 920 m, 17 Jan. 1947, *Vargas 6311* (US). Prov. Paucartambo: Pilcopata, Villa Carmen, 720 m, 17 Nov. 1964, *Vargas 15767* (US); *Prov. La Convencion; Sahuayaco, Río Challpimayo near Pacchar, *Plowman & Davis 4852* (COL, F, GH, K, IAN, MO, P, U, US, USM); *Prov. Paucartambo; near Pilcopata, *Plowman & Davis 5000* (F, GH, K); *Prov. Paucartambo, *Plowman & Davis 5036* GH, K). **Puno:** *near Puno, *Soukup 446* (F). **BRAZIL. Acre:** Rio Acre, Porvir, 14 Nov. 1923, *J. G. Kuhlmann 809* (RB); Rio Acre, Monte Mo, Dec. 1911, *Ule 9750* (G, K, MG). **Mato Grosso:** Arinos, caminho do Porto Velho, Nov. 1914, *J. G. Kuhlmann 1326* (R), *J. G. Kuhlmann 1327-k* (SP, US); Utiarity (Papagaio), Apr. 1918, *J. G. Kuhlmann 2287* (R, RB); Mato próximo do Rio Sacre, 17 Nov. 1944, *A. S. Lima 7859* (SP); *Municipio de Colider; estrada Santarem–Cuiabá, 30 km de Guarantan, Serra do Cachimbo, *I. L. Amaral et al. 803* (F); *Municipio de Colider; estrada Santarem–Cuiabá, Serra do Cachimbo a 30 km da cidade de Guaranta, *M. N. Silva et al. 17* (F). **Pará:** *Alto Tapajos, Rio Cururu, *Anderson 11129* (NY); *Municipio de Castanhal; Colonia 3 de Outubre, *Guedes 265* (IAN); *Belem; IPEAN, *Pires & Silva 11811* (IAN). **Rondônia:** Rio Madeira, Porto Velho, 10 Jan. 1930, *Ducke s.n.* (RB); 8 km NE of Porto Velho, 7 Nov. 1968, *Prance et al. 8265* (WIS); Machado River region, source of Jatuaraha River, Angostura, Dec. 1931, *Krukoff 1532* (NY); *próximo de Vilhena, *Vieira et al. 641* (F). **BOLIVIA. Beni:** *Prov. Ballivián; Río Chimane, environs Fatima, *Davis & Marshall 1106* (F). **Cochabamba:** *Prov. Chaparé; N of Villa Tunari, *Besse et al. 513* (SEL). **La Paz:** Uchimachi–Coroico, 20 Jul. 1894, *Bang 2352* (BM, F, G, GH, K, LE, M, MICH, MO, NY, PH, US, W); Hacienda Simaco sobre el camino a Tipuani, 1400 m, Feb. 1920, *Buchtien 5640* (GH, US); Hacienda Casano, 1,400 m, 27 Jan. 1923, *Buchtien 7615* (GH, UC); near Yungas, 4000 ft, 1885, *Rusby 1030* (F, NY, PH, US); Mapiri, 2,500 ft, May 1886, *Rusby 2611* (NY); Huachi, head of Beni River, 3000 ft, Aug. 1921, *White 1072* (GH, NY); Beni River, Jul. 1886, *Rusby 862* (NY); *Prov. Larecaja; Mapiri, *Beck 4937* (F); *Apolo, Salinas–Yanaloma trail, *Boeke 1477* (F); *Prov. Larecaja, road from Caranavi to Guanay, beyond Alcoche, *Plowman & Davis 5172* (F, GH, K, P, U, USM); *1.8 km SW of Yolosa on road to Chuspipata, *Solomon et al. 12022* (F); *14.3 km SW (above) Yolosa on road to Chuspipata, *Solomon et al. 12071* (F). **Santa Cruz:** Lagunillas, Cordillera of Tucahuasi, 900 m, Aug. 1934, *Cardenas 2813* (F); Prov. Gutierrez, Fraile Buenavista, 450 m, 3 Jan. 1926, *Steinbach 7404* (GH, NY, S).

Brunfelsia mire is a small, unbranched shrub rarely attaining more than 1 m in height. It grows in humid, often swampy forests in deep shade, mostly between 400 and 1400 m elevation. Its area extends along the eastern flank of the Cordillera from central Bolivia to Peru and north and east into parts of Brazil. The flowers are violet and fade to white with age; they appear between November and February.

Still known from relatively few collections, *B. mire* shows considerable variation in the size and shape of the leaves and calyx. Populations from central Bolivia, exemplified by the type collection, have typically large, oblanceolate leaves with divaricating lateral nerves and a relatively short, tubular-campanulate calyx. Populations from Mato Grosso (*J. G. Kuhlmann 1326*) and southern Peru (*Stork et al. 10461*) have ovate-lanceolate leaves with arching, diverging lateral nerves. Still other collections from the state of Acre in Brazil (*Ule 9750, Kuhlmann 809*) and adjacent Peru (*Madison 986*) have oblong to oblanceolate leaves with spreading nerves and a longer, narrowly tubular calyx. These last populations strongly resemble *B. hydrangeiformis* of southeastern Brazil, a closely related species. The full range and nature of variation within *B. mire* is still incompletely known because of the paucity of herbarium material and lack of field studies. At this time, however, it seems best considered as a

polymorphic species exhibiting several different phenotypes in different parts of its range.

The affinities of *B. mire* lie with *B. chiricaspi* of Colombia and *B. hydrangeiformis* of southeastern Brazil, especially *B. hydrangeiformis* subsp. *capitata*. The similarity between the latter species and *B. mire* is striking in certain populations mentioned above and suggests that these plants may have had a more or less continuous distribution at some time in the past. This pattern of distribution is also seen in *B. uniflora* and *B. bonodora–B. grandiflora*. Subsequent differentiation of populations of *B. mire* in western South America has given rise to the heterogeneous complex that we see today. Introgressive hybridization may have occurred with *B. grandiflora*, the flowers of which closely resemble some populations of *B. mire*.

Brunfelsia mire may be distinguished from *B. hydrangeiformis* subsp. *capitata* by the smoother leaves, by the smaller calyx, and by the corolla tube, which is exserted at least twice the length of the calyx.

Brunfelsia mire also shows affinities with *B. chiricaspi*, which also has large oblong-obovate leaves and a corymbiform inflorescence. *Brunfelsia mire* may be distinguished primarily by the longer corolla tube (25–38 vs. 22–25 mm), by the spreading corolla lobes, and by usually having many flowers per inflorescence.

The specific epithet of *B. mire* is taken from the native name of the plant. It is used as a strong medicine by the Indians of central Bolivia to expel cutaneous parasites and has been the object of some pharmacological–pharmacognostic investigation [see Plowman, 1977—Eds.].

20. *Brunfelsia obovata* Benth. in DC., Prodr., 10: 199. 1846. Type: BRAZIL: Minas Gerais, near Parahybuna, 3 ft high in a marsh in water 2 ft deep, 1841, *Gardner 5064* (holotype, K; isotypes, BM, CGE, F, G, GH, K, NY, US 1067018, W).

Franciscea obovata (Benth.) Miers, Ann. Mag. Nat. Hist. Ser. 2, 5: 250. 1850.

Shrub to 1 m tall, much branched. **Branches** spreading, naked, glabrous. **Bark** light brown. **Branchlets** short, slender, sparsely pubescent to villous, yellowish brown. **Leaves** mostly toward the tips of branchlets, rarely scattered, blade 2–9 cm long, 1–3.5 cm wide, obovate to oblong-obovate, blunt to rounded at apex, at times subacute or with short acumen, somewhat revolute at margin, cuneate to narrowed at base, upper surface usually glabrous, smooth, dull, dark green, lower surface rugulose (in siccitate), pubescent-villous, especially at midrib, yellowish green, firmly membranaceous to thickly coriaceous, lateral nerves often obscure, 4–7, straight or somewhat curved; petiole 2–5 mm long, more or less villous, rarely glabrous. **Inflorescence** terminal on current year's branchlets, sessile. **Flowers** 1–10, showy, bluish to lilac, fading to white with age. **Bracts** 2–10 mm long, small, linear-lanceolate, sometimes concave, villous, ciliolate at margin, caducous. **Pedicel** 2–9 mm long, slender, thickened toward apex, angular-grooved, glabrous, rarely glandular. **Calyx** 10–22 mm long, 6–10 mm in diameter, tubular to tubular-campanulate, oblong-ovoid in bud, strongly inflated, 5-angled at sinuses, concave between sinuses at lobes, glabrous, smooth, light green, firmly membranaceous, sometimes striately nerved, teeth short, 1–4 mm long, broadly ovate, rarely lanceolate-ovate, blunt to subacute at apex; calyx in fruit enlarging somewhat to include capsule, nitid, coriaceous, prominently striate-nerved. **Corolla** tube 20–30 mm long, 1.5–2 mm in diameter, 1–3 times as long as calyx, glandular, especially toward apex; limb 25–45 mm long, spreading, lobes 9–16 mm long, broadly rounded. **Stamens** inserted in upper part of corolla tube; upper pair of filaments suberect, 3 mm long, anthers briefly exserted from tube; lower pair included, 2 mm long; anthers 1.5 mm long, reniform. **Ovary** 2 mm long, conical-ovoid; style 18–23 mm long, slender; stigma 1 mm long, briefly bifid, gaping. **Capsule** nearly enclosed by persistent calyx, 8–10 mm long, 8–12 mm in diameter, subglobose, apiculate at apex, rugose (in siccitate), greenish brown, pericarp coriaceous, 0.5–1 mm thick, sparingly dehiscent. **Seeds** 4–8, 4 mm long, 2.5 mm in diameter, oblong, somewhat narrowed at ends, angular, dark, reddish brown, reticulate-pitted. **Embryo** unknown.

DISTRIBUTION—Brazil. See Figure 37.

Key to the Varieties of *Brunfelsia obovata* Benth.

1. Leaves 4–9 cm long, firmly membranaceous to subcoriaceous; flowers (1)2–5; pedicels 1–8 mm long; calyx 16–22 mm long, tubular-in-

FIG. 37. Distribution of *Brunfelsia latifolia* (solid square), *B. macrocarpa* (solid triangle), *B. obovata* (open circle), and *B. pilosa* (solid circle).

flated; corolla tube 1–1½ times as long as calyx ..... 20a. *Brunfelsia obovata* var. *obovata*

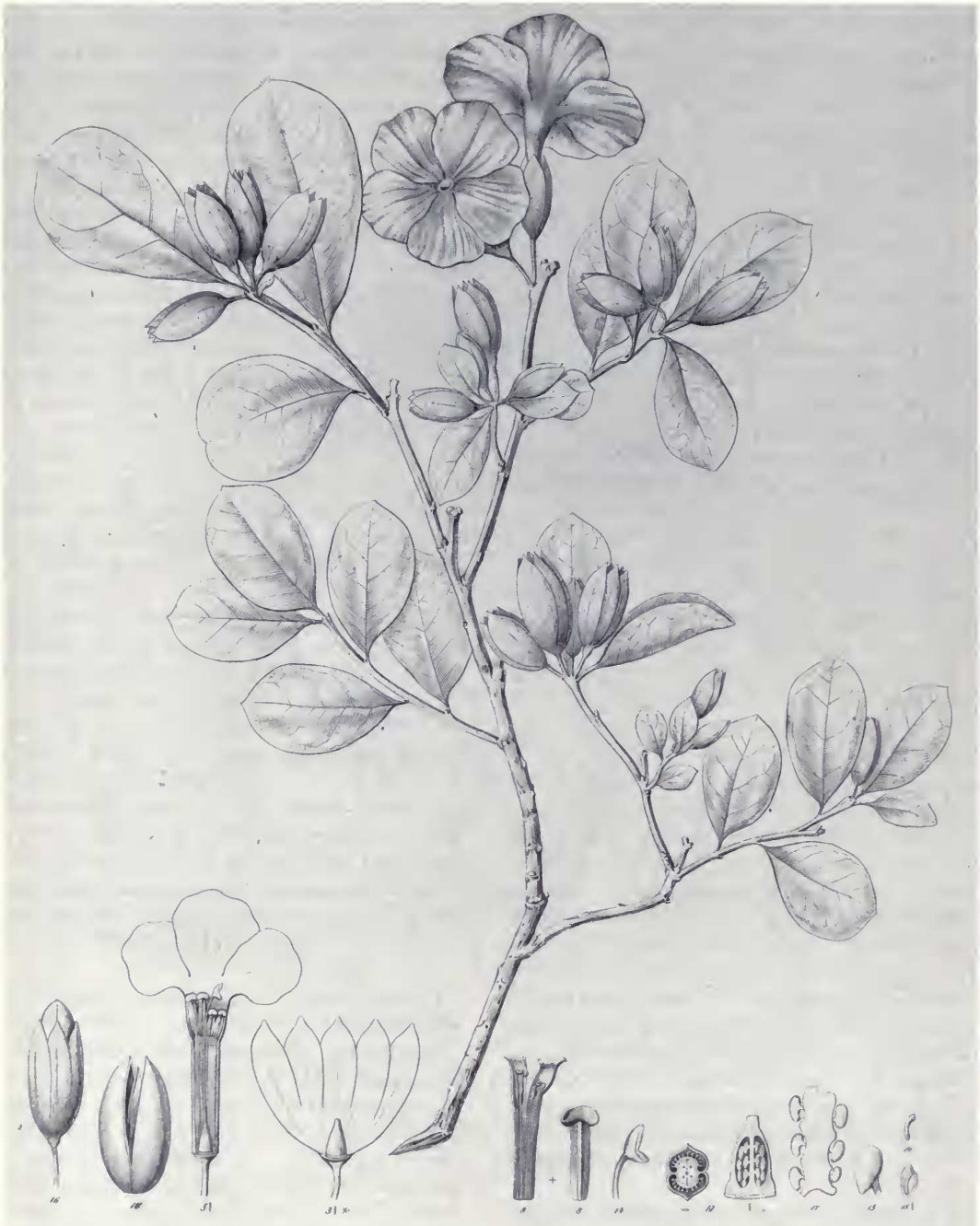
1. Leaves 2.5–7.5 cm long, coriaceous, stiff; flowers 3–10 (rarely reduced to 1–2); pedicels 5–12 mm long; calyx tubular-campanulate; corolla tube 1½–3 times as long as calyx .... 20b. *Brunfelsia obovata* var. *coriacea*

20a. *Brunfelsia obovata* var. *obovata*. Figure 38.

Leaves blunt to rounded at apex, or short acuminate, 4–9 cm long, 1.8–3.5 cm wide, firmly membranaceous to subcoriaceous, with 5–7 lateral nerves. **Flowers** (1)2–5. **Pedicels** 1–8 mm long. **Calyx** 16–22 mm long, tubular. **Corolla** tube 20–25 mm long, 1–1½ times as long as calyx.

DISTRIBUTION—Brazil (Goiás, Minas Gerais, São Paulo).

SPECIMENS EXAMINED—**BRAZIL. Goiás:** *Municipio Alto Paraiso; Chapada dos Veadeiros, *Hatschbach & Kummrow 37257* (GH). **Minas Gerais:** Dist. de Carangola, Alto da Serra da Yrama, 19 Apr. 1935, *J. G. Kuhlmann 141* (RB); Camanducaia, margem do Rio do Sellado, 1800 m, 14 Nov. 1961, *Handro 984* (SP); Sapucai–Mirim, Serra da Mantiqueira, 1400 m, 6 Nov. 1953, *M. Kuhlmann 2926* (SP); without locality, 1816–1821, *St. Hilaire B-2051* (P). **São Paulo:** São Paulo, 1835, *Lund 755* (C, G-DC, non vidi; photographs, F, PH); in silvis paludosis inundatisque pr. São José, pr. São Paulo, Oct.–Nov. 1833, *Riedel 1467* (GH, K, LE); Est. Campo Grande (São Paulo Railway), 17 Nov. 1893, *Edwall 1981 p.p.* (C, SP).



BRUNFELSIA obovata.

20b. *Brunfelsia obovata* var. *coriacea* J. A. Schmidt in Mart., Fl Bras. 8(1): 259. 1864. Type: BRAZIL: Piaui, in silivis ad fl. Gurguea, May 1819, *Martius s.n.* (holotype, M).[14] **Figure 39.**

Brunfelsia silvicola Taub. in Bot. Jahrb. Syst. 21: 450. 1896. Type: BRAZIL: Goias, in silvarum marginibus in ditione fluminis superioris Maranhão, Sep., without year, *Ule 3019* (type destroyed at Berlin). Representative specimen and possible topotype, same locality, Sep. 1892, *Ule 77* (RB-621, P, R-66267).

Leaves 2.5–7.5 cm long, 1–3.3 cm wide, blunt to subacute at apex, coriaceous, with 4–6 lateral nerves. **Flowers** 3–10, rarely 1–2. **Pedicels** 5–12 mm long. **Calyx** 10–16 mm long, tubular-campanulate. **Corolla** tube 20–30 mm long, 1½–3 times as long as calyx.

DISTRIBUTION—Brazil (Bahía, Distrito Federal, Goiás, Piauí).

SPECIMENS EXAMINED—**BRAZIL. Bahía:** Jatoba (Chapada), 1913, *Lützelburg 4019* (M); *Chapadão Occidental da Bahía, 12 km N of Correntina on road to Inhaumas, *Harley 21898* (F). **Distrito Federal:** cerrado perto Corrego Guara, 5 Mar. 1962, *Castellanos 23294* (R); Brasilia, Fundacão Zoobotanica, 8 Sep. 1961, *Heringer 8662* (SP); Sobradinho, 7 Sep. 1962, *Heringer 8993/1197* (SP, US), 21 Mar. 1963, *Heringer 9096/1290* (US); Corrego Samambaia, near Taguatinga, 1100 m, 10 Sep. 1965, *Irwin et al. 8152* (WIS); road Brasilia to Taguatinga, 12 Sep. 1964, *Prance & Silva 59030* (WIS); ca. 5 km S of Brasilia, on road to Belo Horizonte (Rio Gama), 1175 m, 21 Sep. 1965, *Irwin, Souza & Reis dos Santos 8514* (WIS); *Brasilia, *Duarte & Santos 102* (F, NY); *Nucelo Bandeirante, *Heringer 10556* (F); *Bacia do Rio São Bartolomeu, *Heringer et al. 4281* (F); *ca. 5 km SE of Brasilia on road to Belo Horizonte, *Irwin et al. 13126* (F); *Brasilia; Corrego de Bananal, *Plowman 10020* (F). **Goiás:** entre cabeceira do Rio das Pedras et le campement du Corto, 2 Sep. 1893, *Glaziou 21920* (BR, K, LE, P, R); *Chapada dos Veadeiros, *Anderson 6751* (F, MO); *Cristalina, *Hatschbach 43843* (F); *Formosa, *Heringer 10719* (US).

Brunfelsia obovata was described by Bentham in 1846 in de Candolle's *Prodromus*, citing a specimen collected by George Gardner. In the same work, however, he cited *Lund 755*, which also belongs to *B. obovata*, as a syntype of *B. calycina*.

Brunfelsia obovata is a distinct species readily recognized by the obovate, apically blunt leaves and by the inflated, angular calyx. It is closely allied with *B. cuneifolia* of southern Brazil and has been confused with this species. *Brunfelsia cuneifolia* differs in having the leaves cuneate to acuminate at the apex; longer, lanceolate calyx lobes; and a well-developed indument.

From an ecological standpoint, *B. obovata* is somewhat specialized. It is almost always found in aquatic or semi-aquatic environments, often standing in water. It occurs in *brejos* (swampy secondary forest), along the flooded margins of rivers, and in humid *capoeiras*, from about 300 to 1800 m elevation.

Two varieties are distinguished within *B. obovata*. The typical variety occurs in Minas Gerais and São Paulo. Variety *coriacea* grows in the interior states of Goiás and Piuaí and is distinguished by smaller, more coriaceous leaves; more flowers (up to 10) per inflorescence; a shorter calyx (10–16 vs. 16–22 mm); and the corolla tube relatively longer than the calyx (1½–3 vs. 1–1½ times as long). In addition, the calyx of var. *coriacea* is more coriaceous and more strongly angled than in var. *obovata*.

Few collections of *B. obovata* are known, and only one (*St. Hilaire B-2051*) shows characters somewhat intermediate between the two varieties, indicating possible hybridization between them. Variety *obovata* flowers in October and November. Its fruits are as yet unknown. One common name, *broma*, has been reported for the species (Peckolt, 1909).

Brunfelsia obovata var. *coriacea* corresponds

[14] In this thesis (Plowman, 1973) and in the manuscript we received, this taxon was cited as subspecies *coriacea stat. nov.* However, in the herbarium at F, all later aquired collections were annotated by Plowman in the mid-1980s as variety *coriacea* J. A. Schmidt, indicating to us that he had changed his mind as to the status of the taxon. We have chosen to use the status of variety as this was apparently a more recent decision of Plowman's.—*Eds.*

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FIG. 38. *Brunfelsia obovata* var. *obovata*. From Martius, Flora Brasiliensis (1846).

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Brunfelsia obovata ssp. coriacea
dun. det. Timothy Plowman, 1973

Shrub ca. 1.5 m. tall. Corolla violet, fading to pale lavender with age. Periodically flooded marsh, ca. 5 km. S. of Brasília, on road to Belo Horizonte (Rio Gama). Elevation 1175 m.

H. S. Irwin, R. Souza,
R. Reis dos Santos 21 September 1965

Field work conducted with the collaboration of the Universidade de Brasília, Instituto Agronômico do Norte, and the Ministério da Agricultura. Supported in part by funds from the National Science Foundation.

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well to *B. silvicola* published in 1896 by Taubert, which is here placed in synonymy. The type of *B. silvicola* was destroyed in Berlin in 1945, but another collection (*Ule 77*) from the same locality is extant and may serve as a representative collection and may possibly be a topotype.

Brunfelsia obovata var. *coriacea* flowers in the month of September, somewhat earlier than var. *obovata*; fruits have been collected in March. Variety *coriacea* appears to grow under the same ecological conditions as var. *obovata* (swampy areas) but is found in a generally much drier region of *cerrado* vegetation, probably being confined to localized wet areas.

21. *Brunfelsia pauciflora* (Cham. & Schltdl.) Benth. in DC., Prodr. 10: 199. 1846. **Figure 40.**

Franciscea pauciflora Cham. & Schltdl., Linnaea 2: 600. 1827. Type: BRAZIL. E Brasilia meridionali, without locality or date, *Sellow s.n.* (holotype destroyed at Berlin; fragment, F 621699; photographs, F, NY; isotypes, M).

Besleria inodora Vell., Fl. Flum.: 261. 1829 ("1825"), Ic. 6, t. 81. 1831 ("1827"). Lectotype (designated here): plate 81 of Vellozo.

Brunfelsia calycina Benth. in DC., Prodr. 10: 199. 1846. Lectotype (designated here): BRAZIL. Santa Catarina: Insula Santa Catarina, 1832, *Baron de Colchester s.n.* (K). Lectoparatype: BRAZIL. Santa Catarina: Insula Santa Catarina, *Bacle s.n.* (specimen not located). *Lund 755*, also cited by Bentham, is excluded as a type. It is *B. obovata* Benth. var. *obovata*.

Franciscea calycina (Benth.) Miers, Ann. Mag. Nat. Hist. ser. 2, 5: 250. 1850.

Brunfelsia pauciflora var. *calycina* (Benth.) J. A. Schmidt in Mart., Fl. Bras. 8(1): 257. 1864.

Franciscea eximia Scheidw. ex Moore & Ayres, Gard. Mag. Bot. 1: 16. 1850. Lectotype (designated here): Moore & Ayres, Gard. Mag. Bot. 2: 177 + t. 1850. Representative collection: cultivated at Royal Botanic Gardens, Kew, Herbarium Hookerianum, 1867, without collector (K).

Brunfelsia eximia (Scheidw.) Bosse, Handb. Blumeng. 524. 1859.

Brunfelsia calycina var. *eximia* (Scheidw.) L. H. Bailey & Raffill, Stand. Cyclop. Hort. 1: 581. 1914.

Franciscea macrantha Lem., Jard. Fleur. 3: 349, t. 249. 1853. Lectotype (designated here): Lemaire, Jard. Fleur. 3: t. 249. 1853. Representative collection: Royal Botanic Gardens, Kew, cultivated in temperate house, 11 Nov. 1952, *Souster s.n.* (K).

Brunfelsia calycina var. *macrantha* (Lem.) L. H. Bailey & Raffill, Standard Cyclop. Hort. 1: 581. 1914.

Franciscea lindeniana Planch., Belgique. Horticole. 15: 100, t. 16. 1865. Type: Planchon, Belgique. Horticole. 15: 100, t. 16. 1865. Representative collection: Royal Botanic Gardens, Kew, cultivated in temperate house, 16 Jun. 1953, *Souster s.n.* (K) (see Fig. 42).

Brunfelsia lindeniana (Planch.) G. Nicholson, Ill. Dict. Gard. 1: 216. 1884.

Brunfelsia calycina var. *lindeniana* (Planch.) Raffill, Gard. Chron. ser. 3, 83: 370. 26 May 1928.

Brunfelsia calycina var. *floribunda* L. H. Bailey & Raffill, Standard Cyclop. Hort. 1: 581. 1914. Representative collection: New Jersey, Rutherford, cultivated at Julius Roehrs Co., 29 Mar. 1918, *Bailey s.n.* (BH).

Shrub 1–3(5) m tall. **Bark** somewhat smooth or longitudinally cracked, grayish brown. **Branches** sparse, erect or spreading. **Branchlets** stout, glabrous, rarely pubescent or glandular, smooth, dark green. **Leaves** scattered or crowded near branch tips, blade 6.5–16 cm long, 2–6.5 cm wide, oblong to oblong-lanceolate, more rarely elliptic-oblong or obovate-oblong, apically acute to short acuminate, sometimes blunt or emarginate, cuneate to attentuate at base, glabrous, punctate or rarely glandular pubescent beneath, chiefly at midrib, upper surface dark green, dull to nitid, lower surface pale green, firmly membranaceous to subcoriaceous, lateral nerves 5–11, spreading, straight or broadly arching; petiole 5–12 mm long, glabrous or pubescent. **Inflorescence** terminal, sessile or subsessile, with 1–11 flowers. **Flowers** showy, deep, reddish purple fading to pale lavender or white with age, with white spot at mouth sometimes edged with violet. **Bracts** small, 1–3 per flower, 1–8 mm long, linear-lanceolate, concave, narrowly acute apically, glabrous or glandular ciliolate, caducous. **Pedicel** 11–25(35) mm long, stout, broader toward apex, glabrous or sparsely glandular, in fruit becoming thicker and corky-verrucose. **Calyx** 18–32 mm long, 6–10 mm in diameter, tubular, rarely tubular-campanulate or inflated, punctate to glandular pubescent or completely glabrous, firmly membranaceous to subcoriaceous, pale to dark green, teeth 3–8 mm long, ovate to ovate-lanceolate, incumbent, acute to acuminate at apex; calyx in fruit campanulate-urceolate, completely enclosing fruit, becoming slightly larger and thick-coriaceous, conspicuous-

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FIG. 39. *Brunfelsia obovata* var. *coriacea*.

FIG. 40. *Brunfelsia pauciflora*. Reproduced courtesy of the Linnean Society, London.

FIG. 41. Distribution of *Brunfelsia pauciflora* (solid circle) and *B. rupestris* (solid square).

ly striate-nerved with light brown, lenticular-verrucose outgrowths. **Corolla** tube 28–36 mm long, 1.5–3 mm in diameter, 1–2 times as long as calyx, reddish purple above, paler beneath, ring at mouth 4–5 mm long, elliptic, white, sparsely glandular; lobes 15–30 mm long, broadly rounded to subelliptic, rounded-truncate or blunt at apex, somewhat accrescent with age, more or less overlapping laterally. **Stamens** included in upper part of tube; filaments subterete, anteriorly canaliculate, white, upper pair 4–6 mm long, lower pair 2–4 mm long; anthers 1.5–2 mm long, orbicular-reniform, greenish brown. **Ovary** 2–3 mm long, 1.5 mm in diameter, conical-ovoid, pale green; style 25–30 mm long, filamentous, lavender; stigma 1 mm long, briefly bifid, lobes subequal, white. **Capsule** included in calyx, 20–22 mm long, 15–18 mm in diameter, subglobose to ovoid, smooth, light green, pericarp thin, dry at maturity, sparingly dehiscent. **Seeds** 12–30, 5–6 mm long, 2.5–3 mm in diameter, ovoid or oblong, angular, dark, reddish brown, reticulate-pitted. **Embryo** ca. 5 mm long, straight; cotyledons 2–3 mm long, ovate, flat.

DISTRIBUTION—Brazil (Paraná, Rio de Janeiro, Santa Catarina, São Paulo). See Figure 41.

SPECIMENS EXAMINED—**BRAZIL. Paraná:** Ponta Grossa, 16 Oct. 1910, *Dusén 10305* (S), 16 Oct. 1910, *Dusén 10354* (F, GH, MICH, NY, S), 19 Oct. 1911, *Dusén 8679* (S); Carvalho, 18 Nov. 1909, *Dusén 8961* (F, GH, K, L, MICH, MO, NY, P, S), 5 Nov. 1911, *Dusén 13298* (F, GH, K, L, MICH, MO, NY, P, S), 7 Nov. 1911, *Dusén 13327* (F, GH, NY, S); Jaguariahyba, 10 Oct. 1911, *Dusén 13180* (GH, S); Serra do Mar, Itupava, 450 m, 4 Nov.

1915, *Dusén 17301* (GH, NY, S); Mun. São Jose dos Pinhais, Campo Largo da Roseira, 13 Oct. 1946, *Hatschbach 515* (G, US); Mun. Piraguara, Bauhado, 2 Nov. 1948, *Hatschbach 1058* (US); Mun. Campina Grande do Sul: Rio Pardinho, Vertente Altantico, 29 Oct. 1965, *Hatschbach 13055* (F, P, NY, US); Pico Caratuva, 1500–1600 m, 5 Oct. 1967, *Hatschbach 17308* (C, UC); Mun. Morretes, Rio Ipiranga, 29 Nov. 1966, *Hatschbach 15300* (NY, US); Mun. Quatro Barras, Rio Taquari, 8 Oct. 1968, *Hatschbach 19937* (MICH, MO); km 40 da estrada Curitiba–Paranagua, 17 Oct. 1961, *Pabst 5393/Pereira 6066* (F, W); *Quatro Barras, Morro Mae Catiro, *Hatschbach 15071* (MBM); *Campina Grande do Sul, Serra Virgem Maria, *Hatschbach 20304* (MBM); *Municipio São Mateus do Sul; Tezoura, *Hatschbach 22278* (MBM); *Municipio Campina Grande do Sul; Serra Capivari Grande, *Hatschbach 22771* (MBM); *Municipio Cerro Asul; Barra do Turvo, *Hatschbach 32637* (MBM); *Municipio São Jose dos Pinhaes; Guaricana, *Hatschbach 34918* (MBM, MO); *Municipio Morretes; Estrada da Graciosa, Grota Funda, *Hatschbach 40004* (F); *Quatro Barras, Arredores, *Hatschbach 43273* (F); *Municipio São Jose dos Pinhaes; Purgatorio, *Hatschbach 45295* (F); *Municipio Curitiba; Capão do Centro Politecnico, *Hatschbach & Cervi 46844* (F); *Municipio Quatro Barras; Morro do Anhangara, *Kummrow 1575* (F); *Municipio Guaratuba; Serra do Aracatuba, *Kummrow 2420* (F). **Rio de Janeiro:** Alto Macahé de Nova Friburgo, 30 Oct. 1857, *Glaziou 17168* (C, P, R); Serra do Mocoto, Santa Magdalena, 1400 m, Aug. 1940, *Santos Lima s.n.* (RB); Rio de Janeiro, 1867, *Glaziou 811* (BR, C), 1842, *Raben 746* (BR). **Santa Catarina:** Mun. Brusque: Mata de Hoffman, 50 m, 19 Oct. 1950, *Klein 319* (US); Azambuja, 41 m, 25 Nov. 1947, *Reitz 2768* (UC, S); Brusque, 35 m, 25 Nov. 1947, *Reitz C 1952* (S, US); Mato do Malucher, 40–50 m, 23 Feb. 1952, *L. B. Smith 5786* (US). Mun. Itajaí: Itajaí, Morro da Fazenda, 150 m, 3 Nov. 1955, *Klein 1751* (M, US), 17 May 1969, *Plowman 2739* (GH); Itajaí, Sep. 1870, *Mueller 435* (K); Braço Joaquim, Luis Alves, 300 m, 30 Sep. 1954, *Reitz & Klein 2160* (G, US); Ilha de Santa Catarina, Saco Grande, 300 m, 23 Nov. 1966, *Klein & Bresolin 6864* (US). Mun. Bom Retiro, Riozinho, 1000 m, 23 Dec. 1948, *Reitz 2743* (US); pinheiral, 25 Nov. 1956, *Smith, Reitz & Klein 7936* (K, NY, R, US); Mun. Ibirama, Horto Florestal I.N.P., 350 m, 2 Nov. 1953, *Reitz & Klein 1158* (US), 450–700 m, 12 Nov. 1956, *Smith & Klein 7532* (R, US); Blumenau, Mata da Companhia Hering, 300 m, 22 Oct. 1959, *Reitz & Klein 9205* (US). Mun. Rio do Sul, Serra do Matador, 550 m, 17 Oct. 1958, *Reitz & Klein 7329* (US). Joinville, Estrada Dona Franciscea, 450 m, 26 May 1957, *Reitz & Klein 4238* (US), 600 m, 6 Nov. 1957, *Reitz & Klein 5601* (NY, UC, US). **São Paulo:** Moaca, 22 Sep. 1912, *Brade 6036* (S, SP); Mun. Iguapé, Morro das Pedras, Sep. 1920, *Brade 8088* (RB); Iguapé, 20–100 m, Sep. 1901, *Wettstein & Schiffner s.n.* (W); caminho do Porto da Ribeira, 4 Oct. 1894, *Löfgren & Edwall 2705* (SP); Bananal, Serra da Bocaina, Sertão do Rio Vermelho, 1200 m, 7 Oct. 1949, *Brade & Duarte 20119* (GH, RB); Campos do Jordão, Oct. 1937, *Campos Porto 3400* (GH, R), Oct. 1945, *Leite 3660* (A); Mata da Boa Vista, 25 Nov. 1949, *M. Kuhlmann 2176* (SP); Estação Pilar do Sul, 28 Sep. 1898, *Edwall 4329* (SP); São Paulo, Agua Funda, Mata do Instituto de Botânica, 25 Mar. 1965, *Rubens Faria 4* (SP); Jabaquara, 27 Sep. 1945, *Handro s.n.* (SP); Campinas, *Heiner 209* (S), Sep. 1900, *Campos Novaes 214* (US), 18 Aug. 1894, *Campos Novaes 2960* (SP); Butantan, 25 Sep. 1917, *Hoehne 582* (M, SP). Bosque de Saude, 9 Sep. 1922, *Hoehne 7953* (SP, US); Hansa, 24 Oct. 1928, *Hoehne 23169* (SP, US); Jaragua, 10 Oct. 1929, *Hoehne 24405* (SP); Limeira, 30 Aug. 1951, *M. Kuhlmann 2714* (SP); Cordeiropolis, 19 Nov. 1948, *Levy 12* (SP); Araraquara, 28 Sep. 1888, *Löfgren 948* (SP); Piruibe, 1 Nov. 1891, *Löfgren & Cowan 1660* (C, SP); São Bernardo, 18 Sep. 1908, *Puttemans 6135* (SP); Semin. Espirito Santo–Santo Amaro, 18 Oct. 1942, *Roth 356* (SP); Santa Branca, 21 Oct. 1901, *Vert 6152* (SP).

In his *Flora Fluminensis* of 1829,[15] Vellozo included two species of *Brunfelsia* under the genus *Besleria*. One of these, *Besleria inodora*, was described 2 years later as *Franciscea pauciflora* by Chamisso and Schlechtendal from a form of the plant with a glandular-pubescent calyx. This name was transferred to *Brunfelsia* in 1846 by Bentham, who made the combination *B. pauciflora*. The earlier epithet *inodora* of Vellozo cannot be used for this species since it is preoccupied by *B. inodora* Mart. (1847) (= *B. americana*).

In 1846 Bentham published *B. calycina*, which is essentially a glabrous form of *B. pauciflora*. He cited three syntypes. One of these (*Lund 755*) be-

[15] As mentioned in the discussion of *B. bonodora*, there is evidence indicating that Vellozo's work was not offered for sale in 1825, which is the date that appears on the title page, but rather in September–November 1829, which becomes the effective date of publication (Carauta, 1973).

longs to *B. obovata*; another, collected by Baron de Colchester in Ilha Santa Catarina, has been chosen as the lectotype. The third collection (*Bacle s.n.*), also from Santa Catarina, has not been located. Schmidt (1864) reduced *B. calycina* to a variety of *B. pauciflora* in recognition of their similarity.

Owing to its elegant beauty as a conservatory ornamental, *B. pauciflora* was introduced at an early date into European horticulture and become very popular in the mid-1800s. Several new "species" under the genus name *Franciscea* were meagerly described from cultivated forms, including *F. eximia*, *F. macrantha*, and *F. lindeniana*. These names continue to persist in the horticultural literature in various combinations and have created a great deal of confusion in nomenclature. These forms are here considered as cultivars.

Brunfelsia pauciflora is relatively uniform in morphological characters, perhaps reflecting the uniformity of its habitat in coastal, mostly low-elevation, rain forest. Some variation does exist, however, in the number and size of the flowers and in the size of the leaves.

The presence and nature of the indument in *B. pauciflora* has been used to distinguish varieties and to segregate species. The type specimen of *B. pauciflora* has a glandular pubescence in the calyx and pedicels. This form is found primarily inland in the states of São Paulo and Paraná, where precipitation is less than on the coast. *Brunfelsia calycina* and *B. pauciflora* var. *calycina* were based on the more widespread form with a glabrous and perhaps more coriaceous calyx, occurring in coastal forests from Rio de Janeiro south to Santa Catarina.

Closer examination of the nature of the indument shows a continuous range of intermediate forms of pubescence and glaberrity. The calyx may bear small, scattered, punctate dots; very short, scattered, glandular hairs; a well-developed, glandular villosity; or may be completely glabrous. Indeed, some variability in the development and density of the hairs can be found within a single population. Furthermore, the hairs may be shed from the calyx as the fruit develops. Because of the instability of the calyx indument as a taxonomic character in this species, I have not segregated the populations with glabrous calyces as distinct forms or subspecies, as has been done in the past.

Smith and Downs (1966) pointed out two collections (*Reitz 2743*; *Smith, Reitz & Klein 7936*) from the mixed *Araucaria* forests of Santa Catarina as "possible hybrids" (parents unknown). These specimens differ in having a nonglandular villosity on the lower surface of the leaves at the midrib, whereas the calyces are completely glabrous. These forms suggest possible introgression of genes from other species, such as *B. cuneifolia* or *B. brasiliensis*. Both of these species contain a similar, nonglandular pubescence and occur in the *planalto* region of Santa Catarina.

Brunfelsia pauciflora occurs primarily on the Atlantic-facing slope of the Serra do Mar of southeastern Brazil from the State of Rio de Janeiro to Santa Catarina, including the Serra dos Orgãos, Serra de Mantiqueira, Serra de Paranapiacaba, and several lesser *planaltos* and *morros*. Altitudinally, it ranges from near sea level on the coastal plain to about 1500 m at Pico Caratuvain, Paraná. This is exclusively the zone of the *mata pluvial*, the wet tropical rain forest with up to 1600 mm of rainfall annually (Eiten, 1969). A few populations, as mentioned above, occur to the west in the mixed *Araucaria* forests of the *planalto* of Paraná and Santa Catarina.

This species is often found in shade along small streams and ravines, in humid primary and secondary forests, and in other places where the soil is moist but well-drained. It apparently does not survive well when the forest is clear-cut. *Brunfelsia pauciflora* flowers from September to December, with the fruits appearing between January and March. Fruiting specimens are very scarce because the large showy flowers are most often noticed by collectors.

As an ornamental plant, *B. pauciflora* is one of the most important brunfelsias. It is commonly grown in conservatories in the temperate zone and frequently planted in tropical gardens. In limb diameter, the flowers are the largest of the genus, reaching 8 cm across. There is considerable variation in color from deep, reddish purple to deep purple with a white spot or "eye" at the mouth. This spot is often surrounded by a blue-violet band that fades into the purple. The flowers fade rapidly with age to pale lavender or nearly white (but never pure white), with a concomitant increase of up to 1 cm in the diameter of the corolla.

Several cultivars may now be recognized in cultivation. Cultivar "eximia" (*B. eximia* (Scheidw.) Bosse) has medium-sized leaves with an undulate margin and a densely glandular calyx with sharply acuminate teeth. Cultivar "macrantha" (*B. calycina* var. *macrantha* (Lem.) L. H. Bailey and Raffill) is distinguished by large, leathery, plane leaves and by a large, glabrous calyx

and a large corolla up to 8 cm across (Fig. 41). Cultivar "Lindeniana" (*B. lindeniana* (Planch.) G. Nichols) is a form with rosy-lilac flowers and slightly bullate leaves, according to Raffill (1928). Cultivar "floribunda" [*B. calycina* var. *floribunda* L. H. Bailey & Raffill] has smaller, violet flowers (to 3.7 cm across), shiny leaves, and is very free-flowering.

Several of these cultivars represent very old clones, persisting in horticulture since their introduction in the last century. In an attempt to stabilize these names, I have designated as "representative collections" [for style of citation see Fig. 42—*Eds.*] material at the Royal Botanic Gardens at Kew that agrees with the original descriptions of the horticultural forms. A living collection of *Brunfelsia* cultivars is maintained in the Temperate House of Kew, some of which probably represent the original clones of these forms.

22. ***Brunfelsia pilosa*** Plowman, Bot. Mus. Leafl. 24(2): 42. 1974. Type: BRAZIL. Santa Catarina: Mun. São Miguel d'Oeste, forest above Rio Reperiguacu, Peperi, ca. 26°32′S, 53°44′W, 300–400 m, 21 Oct. 1964, *Smith & Reitz 12777* (holotype, GH; isotypes, MO, R, UC). **Figure 43.**

Shrub 0.5–2.0 m tall, diffusely branched from near base. **Branches** spreading and arching, slender, terete, leafy or naked. **Bark** rough, longitudinally cracked, shedding in thin, chartaceous flakes, yellowish brown. **Branchlets** slender, pilose to villous, grayish green, dark purple when young, the epidermis splitting lengthwise. **Leaves** appearing 2-ranked, scattered on branchlets, blade 3–7.5 cm long, 1.3–3 cm wide, narrowly elliptic, oblong-lanceolate or obovate, acuminate at apex, cuneate at base, pilose on both surfaces, primarily at midrib, dull dark green above, pale green beneath, the young leaves dark purple, firmly membranaceous, lateral nerves 6–9, straight, often prominulous above; petiole short, 1–4 mm long, pilose to villous. **Inflorescence** terminal, sessile, usually with 1 flower, rarely 2–3. **Flowers** showy, deep violet fading to pure white with age, odorless. **Bracts** 1–3, 1–8 mm long, linear-lanceolate, pilose to villous, caducous. **Pedicel** 1–3 mm long, stout, pilose; in fruit becoming corky, rugose-verrucose toward apex. **Calyx** 12–19 mm long, tubular-ventricose, appearing campanulate in exsiccati, terete in cross section, sparsely to densely pilose with long weak hairs, rarely glabrous, purplish, drying reddish brown, membranaceous, teeth 4–10 mm long, subequal, lanceolate, acuminate; calyx in fruit persistent, partially enclosing fruit, light green, becoming subcoriaceous, the sinuses becoming more deeply cut. **Corolla** tube 25–32 mm long, 1.5–3.0 mm in diameter, twice as long as calyx, glabrous; limb 30–47 mm in diameter, spreading, thickening at mouth prominent, round, white lobes 10–15 mm long, subequal, the uppermost posterior lobe somewhat larger, broadly rounded. **Stamens** included in uppermost part of corolla tube; filaments slender, glabrous, upper pair 3–4 mm long, lower pair 3–5 mm long; anthers orbicular-reniform, 1–1.5 mm in diameter. **Ovary** 2–2.5 mm long, 1 mm in diameter, conical-ovoid; style 22–26 mm long, slender; stigma 1 mm long, briefly bifid, in the form of forceps. **Fruit** 12 mm long, 10 mm in diameter, ovoid to subglobose, apiculate at apex, smooth, dark green, shiny, pericarp thin-walled, dry at maturity, tardily dehiscent. **Seeds** ca. 10, 5–6 mm long, 2.5–4 mm in diameter, ellipsoid, reticulate-pitted. **Embryo** unknown.

DISTRIBUTION—Brazil (Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), Paraguay, Argentina (Misiones). See Figure 37.

SPECIMENS EXAMINED—**BRAZIL. Paraná:** Curitiba, Bairro São Nicolau, 18 Nov. 1966, *Caprilioni 1659* (US); Itaperussu, 17 Nov. 1908, *Dusén 7077* (GH, S); Jaguariahyva, 25 Oct. 1910, *Dusén 10443* (GH, MICH, NY, S); Tamandare, 4 Oct. 1914, *G. Jönsson 1054a* (F, GH, NY, S); São Matheus, 27 Feb. 1929, *Gurgel s.n.* (RB); Mun. Rio Branco do Sul, São Vicente, 27 Oct. 1967, *Hatschbach 17610* (C, UC); Ponta Grossa, 2 Nov. 1928, *Hoehne 23309* (SP, US); Foz do Iguaçu, Parque Nacional de Iguaçu, 8 Oct. 1946, *J. G. Kuhlmann s.n.* (RB); Ypiranga, 15 Sep. 1934, *Reiss 99* (GH, NY); *Municipio Irati; Fazenda Aleixo, *Carvalho 83* (MBM); *Municipio Ivai; Bom Jardim, *Hatschbach 22383* (NY); *Municipio Curitiba; Rio Atuba, *Hatschbach 25613* (MBM); *Municipio Gal. Carneiro; Iratim, *Hatschbach 28320* (MBM); *Municipio Pitanga; Borboletinha,

→

FIG. 42. Representative specimen of *Brunfelsia pauciflora* cv. "Lindeniana" in the herbarium at Royal Botanic Gardens, Kew.

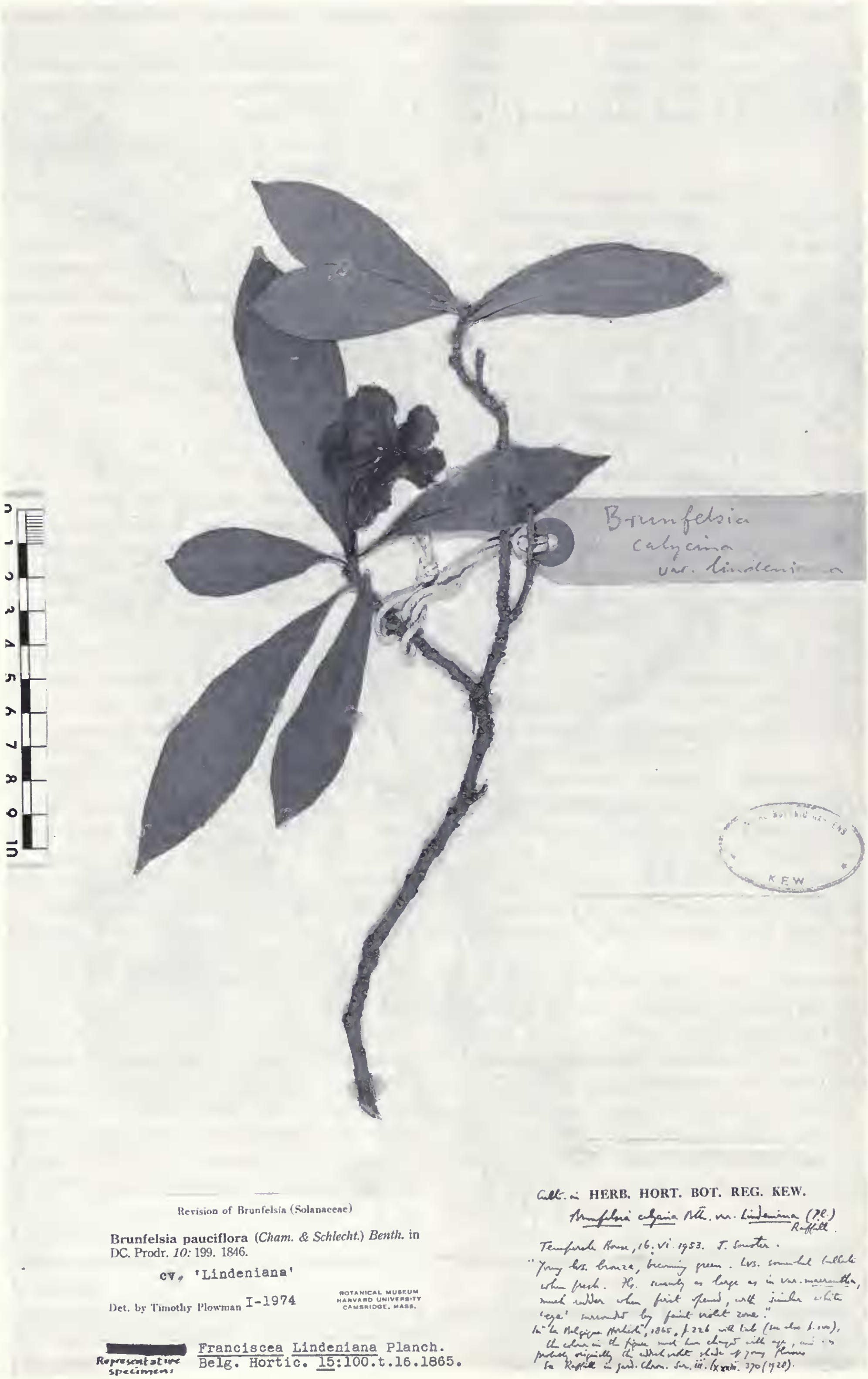
Brunfelsia calycina var. lindeniana
KEW
Revision of Brunfelsia (Solanaceae)
Brunfelsia pauciflora (Cham. & Schlecht.) Benth. in DC. Prodr. 10: 199. 1846.
cv. 'Lindeniana'
Det. by Timothy Plowman I-1974
BOTANICAL MUSEUM HARVARD UNIVERSITY CAMBRIDGE, MASS.
Representative specimen
Franciscea Lindeniana Planch. Belg. Hortic. 15:100.t.16.1865.
HERB. HORT. BOT. REG. KEW.
Temperate House, 16.vi.1953.

FIG. 43. *Brunfelsia pilosa*. Reproduced courtesy of the Botanical Museum of Harvard University.

Hatschbach 32869 (GH); *Municipio Adrianopolis; Rio Pardo, prox. a Barra, *Hatschbach 37876* (MBM); *Municipio Balsa Nova; Campina da Cascavel, *Hatschbach 39164* (GH); *Municipio Tijucas do Sul; Rincão, *Hatschbach 40470* (F); *Municipio Curitiba; Orto Guabirotuba, *Hatschbach 45415* (F); *Municipio Campina Grande do Sul; Belizario, *Hatschbach & Guimarães 15286* (MBM); *Municipio Jaguariaiava; Rio Samambaia, *Hatschbach & Guimarães 25473* (MBM); *Municipio Curitiba; Capanema, *Kummrow 94* (MBM); *near Campo Largo, *Lindeman & Haas 3248* (U, GH, MBM); *Parque Municipio do Iguaçu (Municipio Curitiba), *Oliveira 100* (F). **Rio Grande do Sul:** São Leopoldo, 10 Sep. 1946, *Henz 27246* (MO, NY), 20 m, 17 Sep. 1946, *Henz 35305* (S); Mun. Rio Pardo, Fazenda Horticola, 70 m, Oct. 1923, *Jurgens 19* (B); Colônia Santo Angelo, 4 Feb. 1893, *C. Lindman A-597-b* (S), Sep. 1900, *Schwarzer 50* (L, S); Silveira Martins, 20 Mar. 1893, *C. Lindman A-597-c* (S); Rio dos Sinos, 8 Nov. 1949, *Rambo 44295* (BR, L); Butterberg prope Montenegro, 13 Nov. 1950, *Rambo 49144* (GH, P, W); without locality, 1833, *Gaudichaud 705* (P), 1835, *Isabelle 6* (G); *Municipio Sta. Barbara; Cruz Alta, *Lindeman et al. 8233* (U). **Santa Catarina:** Mun. Caçador, Fazenda dos Carneiros, 1100 m, 7 Dec. 1962, *Klein 3518* (US); Mun. Campos Novos, Palmares, 950 m, 28 Oct. 1963, *Klein 4102* (US); Bituruna, Fazenda Etienne, 11 Feb 1948, *Mello Filho 793* (R); Nova Teutonia, 25 Oct. 1943, *Plaumann 164* (RB); Mun. Araraujа, Rodeio da Areia, 22 Nov. 1943, *Reitz C-171* (RB); Santa Cecilia, 1,100 m, *Reitz & Klein 14136* (NY); Mun. São Miguel d'Oeste, Canela Gaucha, 8 km NW of São Miguel d'Oeste, ca. 26°40′S, 53°34′W, 700–750 m, *Smith & Reitz 12757* (NY, R, US); Mun. Abelardo Luz, N bank of Rio Chapeco at Abelardo Luz, ca. 26°35′S, 52°20′W, 900–1000 m, 23 Oct. 1964, *Smith & Reitz 12870* (C, F, LE, R); Tubarão, Nov. 1889, *Ule 1521* (P). **São Paulo:** Itapetininga, 17 Nov. 1887, *Lofgren 389* (C, R, SP, US); Ypiranga, Nov. 1910, *Luderwaldt 2117* (RB, SP); Campinas, Jundiahy, Mar. 1900, *Campos Novaes 216* (US); Villa de Serra Branca, 1 Nov. 1897, *Puttemans 4328* (SP); Carandiru, Dec. 1912, *Tamandare 244* (RB); Mandaquil, 23 Nov. 1906, *Usteri s.n.* (G). **Without state:** *Sellow 1573* (K, M, W). **PARAGUAY.** In regione fluminis Alto Paraná, Yaguarazapa, 1909–1910, *Fiebrig 5460* (G, GH, US). **ARGENTINA. Misiones:** Dep. San Javiér, Acaragua, 220 m, 30 Sep. 1946, *Bertoni 2974* (B, W); Dep. Candelária: Bompland, 4 Oct. 1909, *Jörgensen s.n.* (BAB), Nov. 1910, *Jörgensen s.n.* (BAB); Santa Ana, Aug. 1901, *Llamas 1530* (BAB, G). Dep. Iguazú: Cataratas de Iguazú, 13 May 1969, *Plowman 2735* (GH); Delícia, camino a El Dorado, 4 Nov. 1949, *Schwindt 2270* (C, LD, NY); Puerto Aguirre, Río Iguazú, 19 Sep. 1922, *I.N.T.A. 4435* (B).

Brunfelsia pilosa is a distinct species related to *B. uniflora* and *B. australis*. Bentham saw a specimen (*Sellow 1573*) referable to the present species but included it within his concept of *B. australis* as a syntype. This specimen is rather exceptional for *B. pilosa* in having a glabrous calyx and leaves. *Brunfelsia pilosa* is distinguished from related species in having very short, stout pedicels (1–3 mm long) and an inflated, tubular calyx with deeply cut teeth (4–10 mm long). The twigs, leaves, and calyx typically contain few to many long, weak trichomes. The flowers are large and showy with a corolla limb nearly 5 cm in diameter.

Brunfelsia pilosa ranges from the Brazilian state of São Paulo south to Rio Grande do Sul and extreme northeastern Argentina (Misiones). It has a fairly wide altitudinal range, occurring from near sea level to 1100 m elevation. In the central part of its range, where it occurs most commonly, this species seems to be associated with the formerly extensive *Araucaria* forests found in the south Brazilian *planalto*.

In contrast to *B. australis*, which may become a small tree, *B. pilosa* grows as a weak shrub with slender, horizontal, arching branches. It occurs primarily in the understory of primary and secondary woods, as well as in thickets and along watercourses. Flowering takes place from October to December with fruits appearing from February to May.

Owing to its attractive flowers, this shrub is cultivated in tropical gardens, although not as extensively as *B. australis*. *Brunfelsia pilosa* appeared in the Florida nursery trade in the mid-1970s and is increasing in importance as an ornamental.

In its native area, *B. pilosa* is known by a variety of common names: *flor de primavera*, *primavera*, *sempre triste*, and *manacá* (Brazil); *azucena silvestre*, *azucena del monte*, and *Jazmin del Paraguay* (Argentina).

23. *Brunfelsia rupestris* Plowman, Fieldiana, Bot. n. s. 8: 7. 1981. Type: BRAZIL. Minas Gerais: Estrada Diamantina a Corinto ate 20 km. Campo rupestre e cerrado. Arbusto ate 2 m, flores roxas. 12 Jan. 1976, *Shepherd, de*

FIG. 44. *Brunfelsia rupestris*. Reproduced courtesy of the Field Museum of Natural History.

Andrade, Konoshita & Tamashiro 3935 (holotype, UEC 11912; isotypes, F 1877095, NY, UEC 11912A). **Figure 44.**

Much-branched **shrub** 1–2 m tall. **Bark** on branches yellowish to reddish brown, cracked longitudinally and transversely, exfoliating in thin flakes. **Branchlets** about 2 mm in diameter, glabrous or puberulent. **Leaves** usually congested near branch tips, short petiolate, blade 10–40 mm long, 6–17 mm wide, lanceolate to oblong, apically acute, sometimes blunt or emarginate, strongly revolute at margin, basally cuneate, glabrous above, puberulent beneath with short

curved glandular or eglandular hairs, shiny, medium green above, dull beneath, drying ochraceous brown, thickly coriaceous, the lateral nerves 4–5, straight, scarcely distinct; petiole 1–3 mm long, glabrous. **Inflorescence** terminal on current season's branchlets, short pedunculate, with 2–5(8) flowers. **Flowers** deep violet with a white "eye" at orifice, fading to lavender with age. **Peduncle** 1–5 mm long, short-branched, the branches articulating with the pedicels, persistent, puberulent. **Bracts** 16 mm long, linear-lanceolate or cymbiform, sparsely villous, ciliolate at margin, caducous. **Pedicel** 4–12 mm long, 1–1.5 mm in diameter, glabrous. **Calyx** 10–15 mm long, 3–6 mm in diameter, tubular-campanulate, terete, glabrous, light green, teeth 2–3 mm long, subequal, ovate to apically acute, the tip itself sometimes blunt or truncate. **Corolla** tube orifice 2–3 mm in diameter; limb 15–22 mm in diameter, spreading, slightly thickened at mouth of tube, lobes 5–10 mm long, subequal, rounded. **Stamens** inserted in upper part of corolla tube; filaments strap-shaped, the anterior pair 2–3 mm long, apically incurved, included, the posterior pair 1–2 mm long; anthers 1.5 mm in diameter, orbicular-reniform. **Ovary** 1.5 mm long, ovoid; stigma 1 mm long, briefly bifid. **Capsule** enclosed by persistent calyx, 16 mm long, 14 mm in diameter, ovoid to globose, apiculate at apex, smooth, pericarp thin, crustaceous, dry at maturity. **Seeds** 5 mm long, 2.5–3 mm in diameter, oblong-ellipsoid, somewhat angular, brown, reticulate-pitted. **Embryo** 4 mm long, straight; cotyledons 2 mm long, ovate.

DISTRIBUTION—Restricted to the *campo rupestre* community in the Serra do Espinhaço, Minas Gerais, Brazil. See Figure 41.

SPECIMENS EXAMINED—**BRAZIL. Minas Gerais:** Serra do Espinhaço, Município Diamantina: Guinda, 5 Nov. 1937, *Mello Barreto 9479* (F, RB), 1300 m, 14 Nov. 1971, *Hatschbach & Pelanda 27941* (GH); ca. 25 km SW of Diamantina on road to Gouveia, 1300 m, 16 Jan. 1969, *Irwin et al. 22077* (F, MO, NY, UB); ca. 12 km SW of Diamantina, 1350 m, 23 Jan. 1969, *Irwin et al. 22465* (NY, UB); Serra do Cruzeiro, 5 Nov. 1979, *V.F. Ferreira et al. 887* (RB); *Municipio Gouveia; Datas, *Hatschbach and Zelma 50296* (F).

Brunfelsia rupestris is a very distinct species that is restricted to the *campos rupestres* at higher elevations in the Serra do Espinhaço of central Minas Gerais. It is most closely related to, and probably derived from, the widespread and polymorphic species *B. brasiliensis*. *Brunfelsia rupestris* differs in having the leaves more congested, thickly coriaceous, strongly revolute at the margins, sparsely pubescent, and with only four to five lateral nerves and in having glabrous pedicels and calyces.

24. *Brunfelsia uniflora* (Pohl) D. Don, Edinburgh New Philos. J. 86. July. 1829. **Figure 45.**

Franciscea uniflora Pohl, Pl. Bras. Ic. 1: 2, t. 1. 1826. Type: BRAZIL. Rio de Janeiro: habitat in umbrosis inter frutices in via a Sumidorio ad Governo et ad Rio Parahybuna, Sep.–Oct. 1818, *Pohl* [9] (holotype, W; isotype, PR).

Franciscea hopeana Hook., Bot. Mag. 55: t. 2829. 1828. Type: Hooker, Bot. Mag. 55: t. 2829. 1828.

Brunfelsia hopeana (Hook.) Benth. in DC., Prodr. 10: 200. 1846.

Brunfelsia hopeana var. *pubescens* Benth. in DC., Prodr. 10: 200. 1846. Type: TRINIDAD. In insula Trinitatis montibus Monos Bocas, without date, *Lockhart 197* (holotype, K; isotype, GOET).

Brunfelsia uniflora var. *pubescens* (Benth.) R. E. D. Baker & N. W. Simmonds in R. O. Williams, Fl. Trinidad and Tobago 2(4): 270. 1953.

Franciscea mutabilis H. Jacq., Ann. Fl. Pomone: 285. Jun. 1842. Type: Jacq., Ann. Fl. Pomone: 285. Jun. 1842.

Brunfelsia mutabilis (Jacq.) Vilm., Rev. Hort. ser. 2, 1: 261. Aug. 1842.

Shrub 0.5–3 m tall with diffuse, spreading branches, often branched from near base. **Branches** slender, terete, becoming somewhat knobby, naked beneath, glabrous. **Bark** grayish brown, shiny. **Branchlets** slender, glabrous or pubescent. **Leaves** scattered along the branchlets, highly variable in size and shape often in the same individual, blade 2.5–8.0 cm long, 1.0–4.0 cm wide, oblong-elliptic, lanceolate or obovate, acute to acuminate at apex, narrowed or cuneate at base, sparsely glandular or variably pubescent beneath at the nerves, or glabrous, dark to light green above, paler green beneath, unusually dull, membranaceous to subcoriaceous, deciduous, lateral nerves 5–8, spreading, straight or arching; petiole short, 1–5 mm long, pubescent or glabrous. **Inflorescence** 1-flowered, terminal, produced at tips of new shoots, sessile, rarely short pedunculate. **Peduncle** 1–6 mm long, slender, terete, glabrous or glandular pubescent, rarely villous, persistent. **Bracts** 1–3, 1–5 mm long, linear-lanceolate, ciliolate, pubescent at midrib, light green, caducous. **Pedicel** 1–6 mm long, erect, glabrous. **Calyx** 8–


Franciscea uniflora.

20 mm long, 3–7 mm in diameter, tubular to tubular-campanulate,[16] narrowed at base, glabrous, rarely with sparse glandular hairs, pale green, membranaceous, teeth 1–3 mm, erect or incumbent, triangular-ovate, acute to acuminate; calyx in fruit coriaceous, striately veined, dark green. **Corolla** tube 13–25 mm long, 1–2 mm diameter, 1–2 times as long as calyx, pentagonal in section, glabrous or sparsely glandular; limb 15–30 mm in diameter, spreading, lobes equal, broadly rounded, at times emarginate, overlapping at the lateral margins, narrowed at base. **Stamens** included in upper part of corolla tube; filaments slender, upper pair 3–5 mm long, lower pair 2–3 mm long; anthers about 1 mm in diameter, orbicular-reniform. **Ovary** 2–3 mm long, 1–1.5 mm in diameter, narrow conical to ovoid; style 15–23 mm long, slender, glabrous; stigma briefly bifid, lobes unequal, obtuse. **Capsule** nearly enclosed by persistent calyx, 7–8 mm long, 8–18 mm in diameter, subglobose to ovoid, smooth, shiny, dark green, pericarp 0.5 mm thick, tardily dehiscent. **Seeds** 10–20, 3–5 mm long, 2–3 mm in diameter, variable in shape, ovoid-ellipsoid, somewhat angulate, dark reddish brown to almost black, reticulate-pitted. **Embryo** 2–4 mm long, curved slightly; cotyledons ovate.

DISTRIBUTION—Venezuela, Trinidad, Guyana, Brazil, Bolivia, Argentina. See Figure 46.

SPECIMENS EXAMINED—**VENEZUELA. Bolívar:** Upata, 1839–1841, *Otto 1003* (W). **Carabobo:** *Entre Trincheras y El Cambur, *Guevara 2276* (F, NY). **Isla Margarita:** El Valle, 300 m, 3 Aug. 1903, *Johnston 71* (GH), 2 Aug. 1901, *Johnston & Miller 265* (GH, NY); without locality, **Facultad Ciencias Forestales s.n.* (NY). **Guarico:** Selvas de Tamanaco, cerca del Cementerio de Paso Real, 11–12 Jun. 1966, *Aristeguieta 6153* (NY, VEN), 21 Sep. 1968, *Plowman 1911* (ECON). **Without state:** Los Cedros, Aug. 1953, *Gines 3605* (US). **TRINIDAD.** Monos Island, 100 ft, Apr. 1936, *Graf 10* (NY). **GUYANA.** Western extremity of Kanuku Mountains, in drainage of Takutu River, 200 m, 4–22 Mar. 1938, *A.C. Smith 3163* (A, B, F, G, LE, MO, NY, P, US, W). **BRAZIL. Bahía:** Espigão Mestre, 6 km S of Cocos, 520 m, 16 Mar. 1972, *Anderson, Steiber & Kirkbride 37048* (WIS); Itambé, Salobinho, basin of Rio Pardo, 14 Nov. 1942, *Fróes 12681/46*; Morro do Chapeu, ca. 7 km S of town of Morro do Chapeu, 1,125 m, 17 Feb. 1971, *Irwin, Harley & Smith 32406* (WIS); Caatinga bei Tamburi, Oct. 1906, *Ule 7061* (K, L); Serra Jacobina, St. Thomé, Ponço d'Areia, 1843, *Blanchet 3862* (BR, G, P); *Blanchet 2616* (P); 1843, *Blanchet s.n.* (C, G, W); without locality, Jun. 1844, *Blanchet s.n.* (G), 1847, *Blanchet s.n.* (G), *Martius s.n.* (L); *Monte Santo, *Harley et al. 16432* (F, K); *Feira de Santana, Serra São Jose, *Noblick 2038* (F); *Barra da Choca, *Santos, T. Soares dos 2511* (F). **Ceará:** Horto Florestal de Ubajara, "Sítio Buriti," 5 Jun. 1942, *Aires do Nascimento 19* (RB); Viçosa de Ceará, 1860, *Allemão 1249* (P, R); Mun. São Gonçalo, near Paracuru, 10 m, 7 Jan. 1945, *Cutler 8271* (MO, US); Guaramiranga, São Salvador, 24 Aug. 1908, *Ducke 1588* (MG); Fortaleza, tabuleiro alem de Aldeota, 5 Feb. 1957, *Ducke 2954* (MG, R, RB); Varzea de Vaca, Feb. 1839, *Gardner 2432* (BM, K); Serra do Bezouro, 20 Jan. 1958, *Guedes 472* (MG); without locality, *Allemão & Cysneiro 1250* (R), 1840, *Gardner 1798* (CGE, F, G, L, NY, P, US, W); *Municipio de São Benedito; Sitio Castelo, Serra da Ipiapaba, *Bezerra 334* (F); *Sitio São Antonio, Serra de Maruoca, *Fernandes, A., s.n.* (F); *Camocim, Cafundo, *S. J. Filho 8* (F). **Espirito Santo:** Bananal, 1924, *Freire 14* (R, US); Gortocazes, 10 Nov. 1943, *J. G. Kuhlmann s.n.* (RB). **Goiás:** Luziana, 18 Sep. 1967, *Heringer 11549* (US). **Minas Gerais:** Viçosa, state agricultural school, 20 Feb. 1959, *Irwin 2674* (F, NY, R, US), 22 Feb. 1959, *Irwin 2701* (F, NY, R, UC); 19 Nov. 1928, *J. G. Kuhlmann s.n.* (RB), 2 Apr. 1935, *J. G. Kuhlmann s.n.* (RB); oxcart road to São Miguel, about km 4, 685 m, 2 Apr. 1930, *Mexia 4551* (GH, US); road to Barrosa, about km 6, 700 m, 15 Oct. 1930, *Mexia 5182* (A, BH, BM, F, G, GB, GH, MICH, MO, NY, PH, S, UC, US); 1827, *Pr. von Nevwied s.n.* (BR). Caldas, 18 Oct. 1854, *Lindberg 203* (BR, S); 25 Sep. 1873, *Mosen 673* (C, LD, P, R, S), 1844–1865, *Regnell I-374* (BR, C, GH, GOET, LE, M, NY,

[16] After completing his thesis, Powman described *B. clandestina*, based on materials he had originally included in *B. uniflora*. The reference to the tubular-campanulate calyx in this description may derive from "*B. clandestina*." See discussion of *B. clandestina*—N.H.

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FIG. 45. *Brunfelsia uniflora* (originally as *Franciscea uniflora*). From Pohl, J. E., Plantarum Brasiliae Icones et Descriptiones (1826).

FIG. 46. Distribution of *Brunfelsia uniflora* (solid circles).

P, R, S, US); Cabo Verde, Oct. 1876, *Barbosa Rodrigues 261* (RB); Parahybuna, Oct. 1840, *Gardner 5062* (BM, CGE, K, P, US, W); without locality, 1858, *Weddell s.n.* (G), 1845, *Widgren s.n.* (BR, LD, S). **Pernambuco:** Isla de Itamarica, Dec. 1839, *Gardner 1095* (BM, CGE, G, NY, P, W); Pernambuco, May 1838, *Gardner s.n.* (BM, K); Cabo Agostinho, 22 May 1952, *D. de A. Lima 52–1039* (R); Olinda, 20 Apr. 1924, *Pickel 670* (SP); Tapera, 18 Dec. 1929, *Pickel 2200* (US). **Rio Grande do Norte:** Monte Alegre, 26 Jan. 1961, *Castellanos 23004* (R); near Natal, Mar. 1914, *Dawe s.n.* (K). **Rio de Janeiro:** Corcovado, Sep. 1833, *Luschnath s.n.* (LE), Nov. 1833, *Luschnath s.n.* (BR, LE), Oct.–Nov. 1832, *Riedel 1112* (LE, NY, P, US, W); Restinga do Leblon, 5 Feb. 1948, *Macedo s.n.* (RB); Parahyba, Oct. 1840, *Gardner 5566* (CGE, GH, K, W); Sobral prope Parahyba do Sul, Nov. 1881, *Schwacke 3311* (GOET, R, US); Estrada de Minas, *Miers 4721* (US); Serra d'Estrella, 1844, *Weddell s.n.* (NY, P); without locality, 1867, *Glaziou 357* (BR); *Municipio São Sabastião do Alto; Fazenda Bahia, *Araujo 968* (F); *Municipio Silva Jardim; Reserva Biológica Poço das Antas, ao Rio Aldeis Velha, *Araujo 3405* (F); *Municipio Nitteroi; Itaipu, Morro das Andorinhas, *Araujo et al. 3202* (F); *entre Itacoatiara e Itaipuacu, Pedra do Alto Mourão, *H. C. de Lima et al. 1637* (CORD, F, K, LA); *Rio de Janeiro, Bairro da Urça, Morro do Pão de Açucar, *Martinelli 5135* (F); *Municipio Casemiro de Abreu; restinga proximo a Rio das Ostras, *Martinelli et al. 5665* (F); *Itaipuacu; Pico Alto Mourão, *Profice et al. 16* (F). **Roraima:** *Boa Vista, Rio Branco, *Fróes 23068* (IAN). Rio Branco, Serra de Carauma, Nov. 1908, *Ule 7715* (K, MG); Road Boa Vista to Venezuela (BR 174);

TABLE 7. Flowering and fruiting times of *Brunfelsia uniflora* in different parts of its geographical range.

Region	Flowering	Fruiting
Venezuela	April–August	August
Northeastern Brazil	December–April	February–May
Southeastern Brazil	October–November	February–April
Bolivia	September–December	Unknown

20 km N of Boa Vista, 1 Feb. 1969, *Prance et al. 9553* (WIS). **São Paulo:** Botucatu, *Edwall 6133* (SP); Campinas, *Heiner s.n.* (S); 2 May 1918, *Campos Novaes 7756* (US); São Jose do Rio Pardo, 1 Oct. 1889, *Löfgren & Edwall 1435* (SP, US); Xiririca, 16 Oct. 1894, *Löfgren & Edwall 2742* (SP, US); BR-2a km 10 antes de Jacupiranga, 15 Oct. 1961, *Pabst & Pereira 6023* (F, R, US); Bananal, Oct. 1833, *Riedel s.n.* (LE, US); pr. São Carlos, Jan. 1834, *Riedel s.n.* (LE); *SW de Jundiai, Serra de Japi, *H. F. Leitão Filho et al. 3219* (F). **Without state:** *Pohl 264* (PR), *Pohl s.n.* (M). **BOLIVIA. Cochabamba:** Prov. Ayopaya, Sailapata, 2,700 m, Dec. 1935, *Cardenas 3380* (GH); Prov. Cochabamba, Siberia, 3,300 m, Jul. 1955, *Cardenas 5216* (L, US); Carrasco, Jatum–Pino, 3300 m, Sep. 1961, *Cardenas 5952* (K, US). **Santa Cruz:** Comarapa, 2800 m, 20 Oct. 1928, *Steinbach 8345* (A, BM, GH, K, MO, NY, S, US); *W of Comarapa on Carretera Fundamental 4, *Davidson 3846* (F). **Without department:** Padcaya–Motoví, 2400 m, 24 Sep. 1927, *Troll 240* (B, M). **ARGENTINA. Jujuy:** Dep. Ledesma, Serranía de Calilegua, 1500 m, 18 Oct. 1963, *Fabris 4502* (M). **Salta:** Orán, cerca del Achiral mas abajo de San Andres, 17–24 Sep. 1873, *Lorentz & Hieronymus 258* (BR, G, LE, P).

Brunfelsia uniflora was first described by Pohl in the genus *Franciscea*. Pohl collected the type in the state of Rio de Janeiro in Brazil. The holotype, bearing the number *9*, is preserved at Vienna (W); a probable isotype with the number *256* is found in Prague (PR). In 1828, Hooker described another species, *F. hopeana*, based on a living plant sent from Brazil, which, according to Hooker, differed from *F. uniflora* in having a shorter corolla tube. D. Don united *Franciscea* with the older genus *Brunfelsia* in 1829, making the correct combination *B. uniflora*. However, Bentham, in his monograph of 1846, used Hooker's specific epithet in the combination *B. hopeana*. This name is still widely, though incorrectly, used for this species, particularly in the horticultural and pharmaceutical literature [see Plowman, 1977—*Eds.*].

Brunfelsia uniflora is the most widespread and variable of the South American species of the genus. It encompasses a heterogeneous complex of forms found throughout eastern Brazil with disjunct populations in Venezuela and Bolivia. While showing some differentiation in response to different habitats and as a result of geographical isolation, the variation is considered to fall within the normal range of a single polymorphic species. The characters and nature of the variability will be discussed according to geographical regions.

Brunfelsia uniflora is distinguished from related species by its smaller, solitary flowers (tube 13–25 mm long), the more or less tubular calyx, and the short (1–3 mm) calyx teeth. It is highly variable in the shape and size of the leaves, in the length of the calyx, and in degree and location of pubescence.

This species grows under diverse environmental conditions throughout its range, which is, in part, responsible for the different phenotypes that are encountered in different areas. It thrives in wet, montane rain forests in Rio de Janeiro and in the high Bolivian *yungas*. It has also become adapted to the drier regions of Minas Gerais, São Paulo, and Ceará, as well as the *cerrado* formations of Goiás and northeastern Brazil. It occurs sporadically as a component of the understory in primary and secondary forests and persists in cut-over areas (*capoeiras*). It grows in different types of soils, including red clay, sand, and moist humus. Altitudinally, *B. uniflora* ranges from sea level to 3300 m in the Andes.

Flowering and fruiting in *B. uniflora* occur at different times of the year in different parts of its range. These are indicated in Table 7.

In the coastal rain forest of Rio de Janeiro and adjacent states, *B. uniflora* assumes its "typical" form, exemplified by the type collection and original description. These plants are very glabrous with obovate-elliptic leaves. The leaves tend to be larger and shinier than in other areas.

Further inland, in the drier highlands of Minas Gerais, there is a tendency toward smaller and more pubescent leaves. In addition the flowers may be short-stalked and the calyx longer and narrower in relation to the corolla tube. Populations showing this trend extend southward in the interior of São Paulo and northward to central Brazil and along the coast to the dry northeast of the country, stopping abruptly in the state of Ceará. Here the plant may become deciduous, flowering at the beginning of the wet season.

Forms similar to those in drier areas of Brazil appear again along the coast of Venezuela, in Isla Margarita and Monos Island (Trinidad). In these northern populations, the young twigs and peduncle, if present, are frequently densely pubescent [perhaps because of environmental conditions; see Knapp, 1989—Eds.]. Bentham tentatively named these plants *B. hopeana* var. *pubescens* pending observation of the corolla, which was missing in his specimen.

When pubescence and calyx length in this form are considered across its entire area, the variation appears more or less continuous, often showing greater differences in adjacent populations than in those separated by thousands of kilometers. The development of pubescence, which may be glandular or nonglandular, is not a good character in this species. The relative length of the calyx is also variable, sometimes appearing tubular-campanulate, sometimes long tubular, with many intermediates. [Later, Plowman differentiated *B. claudestina,* with tubular-campanulate calyx, from *B. uniflora,* with "narrowly tubular calyx." See discussion of *B. claudestina.*—N.H.] In contrast to past treatments of *B. uniflora*, these characters are not considered here for segregating varieties or subspecies.

In southeastern Guyana and adjacent Brazil (Roraima) and southern Venezuela, there occurs another pubescent form of *B. uniflora* but with oblong-ovate leaves, slightly curved, tubular calyces, and hispidulous branchlets. Known only from four collections (*A. C. Smith 3163*, *Ule 7715*, *Otto 1003*, *Prance et al. 9553*), these distinctive populations skirt the eastern part of Guyana Highlands. Their uniformity suggests that they have been isolated from other populations of *B. uniflora* for considerable time.

A final component of *B. uniflora* occurs along the eastern edge of the Bolivian *altiplano* at about 2500 m altitude, extending south into northwestern Argentina. These populations closely resemble plants growing in the coastal rain forest of Rio de Janeiro. They differ in having shiny, coriaceous leaves and longer pedicels. The Bolivian populations grow in very wet, montane cloud forests with *Podocarpus* and *Alnus* and are morphologically homogenous.

In southern Brazil, from the state of São Paulo south to northeastern Argentina, several species occur that may superficially resemble, and have been confused with, *B. uniflora.* Two of these, *B. australis* and *B. pilosa*, are closely related to *B. uniflora* and probably have been derived from it through geographical isolation in the past. They form, in fact, a southern component of what may be referred to as the *B. uniflora* complex.

Both *B. pilosa* and *B. australis* are distinguished from *B. uniflora* by a number of constant morphological characters that are listed under those species. Few or no intermediates or putative hybrids have been found, although their ranges overlap somewhat in São Paulo (*B. uniflora* with *B. pilosa*) and in Rio Grande do Sul (*B. pilosa* with *B. australis*). Schmidt (1864) considered *B. australis* a variety of *B. uniflora*, but he did not see a full range of specimens of either species and included material of *B. guianensis* and *B. pilosa.*

In the states of Paraná and Santa Catarina, two additional species occur that may be confused with the *B. uniflora* complex. Smith and Downs (1966), in the *Flora Ilustrada Catarinense*, assigned specimens of both *B. pilosa* and *B. brasiliensis* subsp. *macrocalyx* to what they considered *B. uniflora.* They further confused *B. cuneifolia* with *B. brasiliensis.* These workers apparently did not examine more typical material of *B. uniflora* and *B. brasiliensis* from farther north.

The breakdown of sharp specific boundaries in these species (especially *B. pilosa*, *B. cuneifolia*, and *B. brasiliensis*) suggests a certain amount of hybridization among them in the past as they came together in the *planalto* of southern Brazil. Subsequent convergence in several characters may also be attributed to a relatively uniform environment in the zone of the *Araucaria* forests. Similarities among these species are particularly noticeable in the size and shape of the leaves, the form and location of pubescence, and in the reduction in the number (often to 1) of flowers per inflorescence. Field studies in which additional collections are correlated with local ecological conditions should prove very useful in understanding their specific relationships.

Brunfelsia uniflora is the source of *manaca* root, which is widely used in Brazil in the treatment of rheumatism and syphilis. It is known by

a number of common names that, along with an account of the uses of the drug, are discussed in Plowman (1977).

Dubious and Excluded Species

Brunfelsia bahiensis Benth. in DC., Prodr. 10: 590. 1846. Type: BRAZIL. Bahía: without locality, 1834, *Blanchet 1509* (holotype, G-DC, non vidi; photographs of holotype, F-645866, NY; isotypes, BM, G, P).

Schmidt considered *B. bahiensis* a dubious species of *Brunfelsia*, and I am inclined to follow suit. It is known only from the type collection. One specimen from Minas Gerais (*Pr. von Nevwied s.n.*, 1816, BR) resembles the type but in fact seems better placed in *B. bonodora.* Another specimen from *Bahía* (*Blanchet s.n.*, 1852, G) is also similar but is considered a form of *B. hydrangeiformis.* Until additional material becomes available, the true affinities of this species must remain in doubt.

Brunfelsia nyctaginoides Standl., Field Mus. Nat. Hist. Bot. ser. 22 (1): 47. 1940. Type: MEXICO. Chiapas: Monte Tacana, 1000–2000 m, Aug. 1938, *Matuda 2411* (holotype, MICH; isotypes, G, K, MICH, MO, NY, US).

This anomalous plant is known only from a few collections on high-elevation, volcanic peaks near the Guatemala–Mexico border. In the original description, Standley (1940) expressed doubt as to the generic placement of this plant. He later recognized its intermediate position between *Browallia*, *Streptosolen*, and *Brunfelsia* (Standley and Steyermark, 1940).

It must, however, be excluded from *Brunfelsia* on the basis of having a broadly lamellate stigma and plicate corolla lobes that are bright scarlet in color, resembling the corolla of *Streptosolen jamesonii. Streptosolen* has a distinctly twisted corolla tube that is lacking in the present plant. Its proper generic disposition must await a thorough evaluation of related genera of the Salpiglossideae. [It has now been placed in the monotypic genus *Plowmania* Hunz. (Hunziker and Subils, 1986).—*Eds.*]

Nomina Nuda

The following names, mostly of horticultural origin, have no taxonomic standing.

Franciscea angusta Heynh., Nom. Bot. Hort. ed. 3. 551. 1850.

Brunfelsia angusta Gentil., Pl. Cult. Serres Jard. Bot. Brux. 40. 1907.

Brunfelsia falcata Regel, Cat. Pl. Hort. Aksakov. 21. 1860.

Brunfelsia gracilis Heynh., Nom. Bot. Hort. ed. 2. 279. 1846.

Franciscea gracilis W. Baxt. in Loud., Hort. Brit. Suppl. 3. 551. 1850.

Brunfelsia latifolia Steud., Nom. Bot. ed. 2. 231. 1840. Non *B. latifolia* (Pohl) Benth.

Brunfelsia lockhartii Heynh., Nom. Bot. Hort. ed. 2. 79. 1846.

Brunfelsia magnifica Gentil., Pl. Cult. Serres Jard. Bot. Brux. 40. 1907.

Brunfelsia montana Lodd., Cat. Pl. ed. 12. 4. 1820.

Brunfelsia multiflora Regel, Cat. Pl. Hort. Aksakov. 21. 1860.

Brunfelsia schomburgkiana Klotsch ex Schomburgk, Versuch. Fauna Fl. Br. Guy. 1155. 1848.

Brunfelsia sieberi Regel., Cat. Pl. Hort. Aksakov. 21. 1860.

Brunfelsia spinosa Jacq., Enum. Syst. Pl. 14. 1760.

Brunfelsia spruceana J.A. Schmidt in Mart., Fl. Bras. 8(1): 258. 1864. A nomen nudum placed in the synonymy of *B. maritima* Benth. by Schmidt.

Franciscea pohliana Heynh., Nom. Bot. Hort. ed. 2. 1846.

Martia opifera Lacerda ex J. A. Schmidt in Mart., Fl. Bras. 8(1): 261. 1864. A nomen nudum placed in the synonymy of *B. hopeana* (Hook.) Benth. by Schmidt.

XI. Editors' Acknowledgments

It is impossible for us to acknowledge with certainty all those whom Timothy Plowman would have wished to thank for their help. Because this work is based primarily on his Ph.D. dissertation, the original acknowledgments to individuals are reprinted here. We extend our apologies to anyone who should be mentioned but is not.

As editors, we would like to add our own acknowledgments, especially to Dr. Michael Dillon of the Field Museum of Natural History, Chicago, who originally suggested taking on the task of preparing this revision for publication and who

patiently answered all our queries and requests for advice. Nancy Hensold and Christine Niezgoda, also of the Field Museum, gave us invaluable aid in searching Plowman's notes and other archival material and provided additional data. Several individuals and organizations kindly gave us permission to reproduce previously published illustrations: *Curtis's Botanical Magazine*; the Field Museum of Natural History, Chicago; the Botanical Museum, Harvard University; Christabel King; and the Linnean Society, London. The drawing of *Brunfelsia amazonica* was prepared by Margaret Tebbs, and all the distribution maps were prepared by Malcolm Penn. Kai Vollesen of the Royal Botanic Gardens, Kew, provided the photograph of *B. obovata* cv. Lindeniana, and Dr. Jim Mallet of University College, London, provided the photograph of *Methona* larvae. The Photographic Unit at the Natural History Museum produced several of the figures published here, and Marian Short checked the manuscript.

XII. Plowman's Acknowledgments

The following acknowledgments are from Timothy Plowman's dissertation:

Many persons have generously given to me their time and assistance during the course of this study. I gratefully acknowledge their help, which has both enhanced the quality and facilitated the completion of this work.

I would especially like to express my sincere gratitude to Prof. Richard Evans Schultes, who first suggested the genus *Brunfelsia* as a problem in ethnopharmacology and provided continued support and encouragement throughout the study. His profound interest in the plants and the people of South America demonstrated to me the importance of field studies in ethnobotanical and taxonomic research.

During the course of my field work, many individuals graciously offered their facilities and hospitality, food, and lodging, and generally made my travels more pleasant and scientifically rewarding. I am particularly indebted to the following persons: Dr. Leandro Aristeguieta in Venezuela; Drs. Jesús Idrobo, Eduardo Mora Osejo, and Álvaro Fernández, Sr. Rafael Wandurraga, and Sr. Pedro Juajibioy Chindoy in Colombia; Dr. Ramon Ferreyra and Sr. Fernando Tina in Peru; Dr. Julián Cámara Hernández and Drs. Antonio and Carmen Krapovickas in Argentina; Dr. Roberto Klein and Sr. Dimitri Sucre in Brazil; Drs. George R. Proctor and C. D. Adams in Jamaica; and Dr. Roy Woodbury in Puerto Rico.

The following made many useful suggestions and criticisms and assisted in solving taxonomic problems: Dr. Cleofé Calderón, Dr. José Cuatrecasas, Dr. William T. Gillis, Dr. Leslie A. Garay, Mr. William Grimé, Prof. Richard A. Howard, Mr. Tom E. Lockwood, Prof. Robert F. Raffauf, Prof. Reed C. Rollins, Dr. Velva E. Rudd, Dr. Elizabeth A. Shaw, Dr. Bernice G. Schubert, Dr. Lyman B. Smith, Dr. Thomas R. Soderstrom, Dr. William T. Stearn, Prof. Rolla M. Tryon, Prof. Carroll E. Wood, and Dr. John J. Wurdack.

Technical assistance was provided by Drs. Alice F. Tryon, Umesh Banerjee, and Ihsan Al-Shehbaz and Mr. Gilbert Pierce.

Dr. Fred Barkley and Mr. Eugene Courtney at the Botanical Research Station in Woburn, Massachusetts, Mr. Al Fordham of the Arnold Arboretum, and Mr. Conrad Smith of Harvard University provided much help with the care of living material.

Bibliographic services and many kindnesses were provided by the staff of the libraries of the Gray Herbarium and Arnold Arboretum, particularly Mrs. Patricia Hall, and by Mrs. Mary Gaudet, Mrs. Lilian Hanscom, and Miss Esther Reynolds of the Botanical Museum.

I would also like to thank Ms. Lynda Bates and Judith Gronim for the line drawings that appear in the text, and Mr. Coburn Bennett, Ms. Amina Anderson, and Mr. John Lupo, who were of invaluable assistance with the photographic work.

This study was supported in part by grants from the National Defense Education Act Title IV Fellowship and National Institutes of Health Training Grant (T-01 GM 00036). Field work was partly funded through the Evolutionary Biology Committee, Harvard University (National Science Foundation Training Grant GB-7346), and the generosity of Mrs. Edward C. Sweeney.

I am grateful to the curators of the herbaria mentioned in the text, who lent specimens of *Brunfelsia* used in this study.

Lastly I would like to express my deep gratitude to my parents, Dr. and Mrs. J. Wesley Plowman, who have continuously supported and encouraged me.

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Appendix I: List of Exsiccatae

Acosta Solis 7576 (*grandiflora* subsp. *grandiflora*)
Aguilar 1302 (*australis*), *841* (*australis*)
Aires do Nascimento 19 (*uniflora*)
Albuquerque et al. 1269 (*grandiflora* subsp. *grandiflora*)
Allard 21176 (*grandiflora* subsp. *grandiflora*), *22096* (*grandiflora* subsp. *schultesii*)
Allemão 1249 (*uniflora*)
Allemão & Cysneiro 1250 (*uniflora*)
Almeida 1286 (*brasiliensis* subsp. *brasiliensis*)
Alston & Lutz 138 (*latifolia*)
Amaral, A. s.n. (*brasiliensis* subsp. *brasiliensis*)
Amaral, I. L., et al. 803 (*mire*)
Anderson 11129 (*mire*), *6751* (*obovata* var. *coriacea*), *8949* (*brasiliensis* subsp. *brasiliensis*)
Anderson et al. 37048 (*uniflora*)
Andrade 1024 (*brasiliensis* subsp. *brasiliensis*)
Angeli 250 (*brasiliensis* subsp. *brasiliensis*)
Aparicio & Edmundo 868 (*hydrangeiformis* subsp. *capitata*)
Araujo 3405 (*uniflora*), *954* (*hydrangeiformis* subsp. *hydrangeiformis*), *968* (*uniflora*)
Araujo & Kennedy 24 Mar. 1971 (*latifolia*)
Araujo et al. 3202 (*uniflora*)
Aristeguieta 1669 (*grandiflora* subsp. *schultesii*), *6153* (*uniflora*)
Assis 102 (*brasiliensis* subsp. *brasiliensis*), *137* (*brasiliensis* subsp. *brasiliensis*), *142* (*brasiliensis* subsp. *brasiliensis*), *181* (*brasiliensis* subsp. *brasiliensis*)
Atamp. (?) 6560 (*brasiliensis* subsp. *brasiliensis*)
Bailey & Bailey 758 (*brasiliensis* subsp. *brasiliensis*)
Baker 61 (*grandiflora* subsp. *grandiflora*)
Balansa 2240 (*australis*)
Balgooy 1592 (*australis*)
Bang 1398 (*grandiflora* subsp. *schultesii*), *2352* (*mire*)
Barbosa Rodrigues 261 (*uniflora*)
Barclay 911 (*macrocarpa*)
Barreto 7787 (*brasiliensis*), *7790* (*brasiliensis*), *9749* (*brasiliensis* subsp. *macrocalyx*)
Beck 13335 (*grandiflora*), *4937* (*mire*)
Beck & Liberman 9379 (*boliviana*)
Bedi s.n. (*uniflora*)
Belshaw 3130 (*grandiflora* subsp. *schultesii*)
Bernardi 18138 (*australis*), *20495* (*australis*), *3310* (*grandiflora* subsp. *schultesii*)
Bertoni 2939 (*australis*), *2974* (*pilosa*), *3434* (*australis*)
Besse et al. 513 (*mire*)
Beyrich s.n. (*brasiliensis* subsp. *brasiliensis*)
Bezerra 334 (*uniflora*)
Black 48-2905 (*amazonica*)
Blanchet 1455 (*clandestina*), *2616* (*uniflora*), *3352* (*clandestina*), *3354* (*clandestina*), *3862* (*uniflora*), *Jun. 1844* (*uniflora*), *s.n.* (*clandestina*), *s.n.* (*clandestina*), *s.n. 1843* (*clandestina*), *s.n. 1847* (*uniflora*), *s.n. 1857* (*hydrangeiformis* subsp. *hydrangeiformis*)
Blanco 826 (*imatacana*)
Boeke 1224 (*grandiflora* subsp. *grandiflora*), *1477* (*mire*)
Boer 1047 (*guianensis*)
Bonpland 528 (*australis*)
Bornmuller 219 (*australis*)
Bowie & Cunningham 100 (*hydrangeiformis* subsp. *hydrangeiformis*), *228* (*brasiliensis* subsp. *brasiliensis*)
Brade 10569 (*brasiliensis* subsp. *brasiliensis*), *10583* (*brasiliensis* subsp. *brasiliensis*), *14074* (*brasiliensis* subsp. *macrocalyx*), *18643* (*bonodora*), *18785* (*brasiliensis* subsp. *brasiliensis*), *20953* (*brasiliensis* subsp. *macrocalyx*), *21218* (*brasiliensis* subsp. *brasiliensis*), *6036* (*pauciflora*), *6037* (*brasiliensis* subsp. *macrocalyx*), *7625* (*brasiliensis* subsp. *macrocalyx*), *8088*

(*pauciflora*), *Oct. 1928* (*hydrangeiformis* subsp. *capitata*)
Brade & Duarte 20119 (*pauciflora*)
Brade & Tamandare 6576 (*brasiliensis* subsp. *macrocalyx*)
Braga 1169 (*brasiliensis* subsp. *brasiliensis*), *182* (*brasiliensis* subsp. *brasiliensis*), *203* (*brasiliensis* subsp. *brasiliensis*)
Brandão 2066 (*brasiliensis* subsp. *brasiliensis*)
Bristan 1220 (*chocoensis*), *566* (*chocoensis*), *569* (*chocoensis*)
British Guiana Forest Department 4422 (*martiana*)
Brooke 5653 (*boliviana*)
Brunet sp. nov. 1888 (*hydrangeiformis* subsp. *capitata*)
Buchtien 1299 (*grandiflora* subsp. *schultesii*), *1300* (*grandiflora* subsp. *schultesii*), *2029* (*grandiflora* subsp. *schultesii*), *5640* (*mire*), *7615* (*mire*)
Bunting et al. 10351 (*hydrangeiformis* subsp. *hydrangeiformis*)
Burchell 1372 (*brasiliensis* subsp. *brasiliensis*), *8494* (*burchellii*), *8653* (*burchellii*), *8752* (*burchellii*)
Buttura 157 (*australis*)
Camargo 2123 (*cuneifolia*), *3 Oct. 1957* (*cuneifolia*)
Campos Novaes 214 (*pauciflora*), *216* (*pilosa*), *2960* (*pauciflora*), *7756* (*uniflora*)
Campos Porto 173 (*brasiliensis* subsp. *macrocalyx*), *1879* (*hydrangeiformis* subsp. *capitata*), *3381* (*brasiliensis* subsp. *brasiliensis*), *3400* (*pauciflora*), *s.n.* (*brasiliensis* subsp. *brasiliensis*)
Capanema s.n. (*brasiliensis* subsp. *brasiliensis*)
Caprilioni 1659 (*pilosa*)
Carauta 2420 (*brasiliensis* subsp. *brasiliensis*)
Carauta & de Oliveira 1523 (*brasiliensis*)
Cardenas 2813 (*mire*), *3380* (*uniflora*), *5216* (*uniflora*), *5952* (*uniflora*)
Carvalho 83 (*pilosa*)
Carvalho & Gatti 795 (*clandestina*)
Castellanos 23004 (*uniflora*), *23294* (*obovata* var. *coriacea*), *23973* (*brasiliensis* subsp. *brasiliensis*)
Cavalcante 2518 (*guianensis*)
Chiar s.n. (*australis*)
Claussen 146 (*brasiliensis* subsp. *brasiliensis*), *147* (*brasiliensis* subsp. *brasiliensis*), *157* (*brasiliensis* subsp. *brasiliensis*), *201* (*hydrangeiformis* subsp. *hydrangeiformis*), *334* (*brasiliensis* subsp. *brasiliensis*), *Nov. 1839* (*hydrangeiformis* subsp. *hydrangeiformis*), *Nov. 1842* (*hydrangeiformis* subsp. *capitata*), *s.n.* (*brasiliensis* subsp. *brasiliensis*), s.n. (*hydrangeiformis* subsp. *hydrangeiformis*), *s.n. 1841* (*hydrangeiformis* subsp. *hydrangeiformis*)
Constantino Nov. 1931 (*brasiliensis* subsp. *brasiliensis*)
Correa & Dressler 471 (*dwyeri*)
Croat 13072 (*dwyeri*), *36856* (*australis*)
Cuatrecasas 10611 (*grandiflora* subsp. *schultesii*), *10795* (*grandiflora* subsp. *schultesii*), *11275* (*grandiflora* subsp. *schultesii*)
Curran 619 (*brasiliensis* subsp. *brasiliensis*), *623* (*brasiliensis* subsp. *brasiliensis*), *s.n.* (*australis*)
Cutler 8271 (*uniflora*)
D'Arcy 3959 (*dwyeri*)
D'Arcy et al. 3948 (*dwyeri*)
Davidse & Ramamoorthy 10709A (*brasiliensis* subsp. *brasiliensis*)
Davidse et al. 11611 (*brasiliensis*)
Davidson 3846 (*uniflora*)
Davis & Marshall 1106 (*mire*)
Davis & Yost 958 (*grandiflora* subsp. *schultesii*)
Dawe 241 (*grandiflora* subsp. *schultesii*), *Mar. 1914* (*uniflora*)
Dobereiner & Tokarnia 732 (*cuneifolia*), *841* (*australis*)
Dodson 2822 (*grandiflora* subsp. *schultesii*)
Drummond 7330 (*grandiflora* subsp. *schultesii*)
Duarte 2029 (*brasiliensis* subsp. *brasiliensis*), *5477* (*bonodora*), *631* (*brasiliensis* subsp. *brasiliensis*), *8445* (*hydrangeiformis* subsp. *hydrangeiformis*), *8741* (*brasiliensis* subsp. *brasiliensis*)
Duarte & Pereira 22 Oct. 1964 (*hydrangeiformis* subsp. *hydrangeiformis*), *9 Dec. 1948* (*hydrangeiformis* subsp. *capitata*)
Duarte & Santos 102 (*obovata* var. *coriacea*)
Duarte de Barros 1195 (*brasiliensis* subsp. *brasiliensis*)
Ducke 2954 (*uniflora*), 430 (*amazonica*), 865 (*grandiflora* subsp. *schultesii*), *29 Nov. 1928* (*hydrangeiformis* subsp. *capitata*), *10 Jan. 1930* (*mire*), *s.n.* (*amazonica*), *s.n.* (*guianensis*), *s.n.* (*martiana*)
Ducke & Kuhlmann s.n. (*brasiliensis* subsp. *brasiliensis*)
Duke 11351 (*chocoensis*), *13331* (*chocoensis*), *16047* (*chiricaspi*), *5300* (*chocoensis*), *9429* (*dwyeri*)
Dupre s.n. 1842 (*brasiliensis* subsp. *brasiliensis*)
Dusén 10305 (*pauciflora*), *10354* (*pauciflora*), *10443* (*pilosa*), *13180* (*pauciflora*), *13298* (*pauciflora*), *13327* (*pauciflora*), *13562* (*brasiliensis* subsp. *macrocalyx*), *17301* (*pauciflora*),

2023 (*brasiliensis* subsp. *macrocalyx*), *3388* (*brasiliensis* subsp. *macrocalyx*), *569* (*brasiliensis* subsp. *macrocalyx*), *7077* (*pilosa*), *8679* (*pauciflora*), *8961* (*pauciflora*)

Dwyer 7280 (*dwyeri*)

Dwyer & Gauger 7349 (*dwyeri*)

Dwyer et al. 5051 (*dwyeri*)

Edwall, 15183 (*hydrangeiformis* subsp. *capitata*), *1981 p.p.* (*brasiliensis* subsp. *macrocalyx*), *1981 p.p.* (*obovata* var. *obovata*), *4329* (*pauciflora*), *6133* (*uniflora*)

Elburg 9819 (*guianensis*)

Emmerich 985 (*brasiliensis* subsp. *brasiliensis*)

Engler 1006 (*brasiliensis* subsp. *brasiliensis*), *1009* (*brasiliensis* subsp. *brasiliensis*), *s.n.* (*brasiliensis* subsp. *brasiliensis*)

Escobar 359 (*dwyeri*)

Fabris 4502 (*uniflora*)

Facultad Ciencias Forestales s.n. (*uniflora*)

Farney et al. 584 (*brasiliensis* subsp. *brasiliensis*), *597* (*brasiliensis*)

Fernandes, A., s.n. (*uniflora*)

Fernandez 365 (*macrocarpa*)

Ferreira & Costa 16 (*grandiflora* subsp. *grandiflora*)

Ferreira, V.F., et al. 887 (*rupestris*)

Ferreyra 4760 (*grandiflora* subsp. *schultesii*), *7778* (*grandiflora* subsp. *schultesii*), *985* (*grandiflora* subsp. *grandiflora*)

Fiebrig 49 (*australis*), *5460* (*pilosa*)

Filho S. J. 8 (*uniflora*)

Filho et al. 3219 (*uniflora*)

Flaster 56 (*hydrangeiformis* subsp. *capitata*)

Florschütz & Maas 2924 (*guianensis*), *3094* (*guianensis*)

Forestry Department of British Guiana 7495 (*guianensis*)

Franklin & Glaziou 5319 (*hydrangeiformis* subsp. *capitata*)

Frenzel 666 (*cuneifolia*)

Fróes 11620 (*burchellii*), *12681\46* (*uniflora*), *20067* (*clandestina*), *20210* (*clandestina*), *20535* (*amazonica*), *23068* (*uniflora*), *23974* (*grandiflora* subsp. *schultesii*), *24035* (*grandiflora* subsp. *schultesii*), *25650* (*martiana*), *28393* (*martiana*)

Garcia Barriga 4586 (*grandiflora* subsp. *schultesii*)

Gardner, G. 1095 (*uniflora*), *1798* (*uniflora*), *2432* (*uniflora*), *248* (*brasiliensis* subsp. *brasiliensis*), *5062* (*uniflora*), *5063* (*brasiliensis* subsp. *brasiliensis*) *5065* (*hydrangeiformis* subsp. *hydrangeiformis*), *5566* (*uniflora*), *563* (*hydrangeiformis* subsp. *capitata*), *564* (*brasiliensis* subsp. *brasiliensis*) *May 1838* (*uniflora*)

Gaudichaud 442 (*brasiliensis* subsp. *brasiliensis*), *705* (*pilosa*)

Gehrt 3667 (*brasiliensis* subsp. *brasiliensis*)

Gentry 16249 (*grandiflora* subsp. *schultesii*)

Gentry & Clewell 7138 (*chocoensis*)

Gentry et al. 15707 (*grandiflora* subsp. *schultesii*), *18573* (*grandiflora* subsp. *schultesii*), *18664* (*grandiflora* subsp. *schultesii*)

Germain 171 (*brasiliensis* subsp. *brasiliensis*)

Gill 45 (*grandiflora* subsp. *schultesii*)

Gines 3605 (*uniflora*)

Ginzberger 93 (*brasiliensis* subsp. *macrocalyx*)

Glaziou 11392 (*hydrangeiformis* subsp. *hydrangeiformis*), *11393* (*hydrangeiformis* subsp. *hydrangeiformis*), *11394* (*brasiliensis* subsp. *brasiliensis*), *11395* (*brasiliensis* subsp. *macrocalyx*), *12110* (*australis*), *13478* (*brasiliensis* subsp. *macrocalyx*), *14171* (*brasiliensis* subsp. *brasiliensis*), *14172* (*brasiliensis* subsp. *macrocalyx*), *14173* (*hydrangeiformis* subsp. *capitata*), *14174* (*hydrangeiformis* subsp. *capitata*), *15132* (*brasiliensis* subsp. *brasiliensis*), *15311* (*brasiliensis* subsp. *brasiliensis*), *17168* (*pauciflora*), *17169* (*brasiliensis* subsp. *macrocalyx*), *17170* (*brasiliensis* subsp. *brasiliensis*), *21920* (*obovata* var. *coriacea*), *357* (*uniflora*), *4909* (*hydrangeiformis* subsp. *capitata*), *5970* (*latifolia*), *6908* (*brasiliensis* subsp. *macrocalyx*), *811* (*pauciflora*), *812* (*brasiliensis* subsp. *brasiliensis*), *9558* (*hydrangeiformis* subsp. *capitata*)

Góes & Constantino 543 (*brasiliensis* subsp. *brasiliensis*), *883* (*brasiliensis* subsp. *brasiliensis*)

Graf 10 (*uniflora*)

Granville 1378 (*guianensis*), *2204* (*guianensis*), *2224* (*guianensis*), *B-4854* (*guianensis*)

Guèdes 265 (*mire*), *472* (*uniflora*)

Guevara 2276 (*uniflora*)

Guillemin 41 (*brasiliensis* subsp. *brasiliensis*), *171* (*brasiliensis* subsp. *brasiliensis*), *825* (*brasiliensis* subsp. *brasiliensis*), *954* (*brasiliensis* subsp. *brasiliensis*)

Gurgel 27 Feb. 1929 (*pilosa*)

Handro 27 Sep. 1945 (*pauciflora*), *984* (*obovata* var. *obovata*)

Harley 21898 (*obovata* var. *coriacea*)

Harley et al. 16432 (*uniflora*)

Harling & Andersson 11724 (*grandiflora* subsp. *schultesii*), *11771* (*chiricaspi*), *11804* (*chiricaspi*), *13906* (*grandiflora* subsp. *grandiflora*), *13934* (*grandiflora* subsp. *grandiflora*)

Harling et al. 7021 (*chiricaspi*), *7151* (*chiricaspi*), *7474* (*grandiflora* subsp. *schultesii*), *7700* (*grandiflora* subsp. *schultesii*), *7772* (*chiricaspi*)
Hashimoto 1 (*brasiliensis* subsp. *brasiliensis*)
Hassler 12559 (*australis*), *725* (*australis*)
Hatschbach 1058 (*pauciflora*), *11878* (*brasiliensis* subsp. *macrocalyx*), *13055* (*pauciflora*), *15071* (*pauciflora*), *15159* (*cuneifolia*), *15300* (*pauciflora*), *17308* (*pauciflora*), *17610* (*pilosa*), *18747* (*brasiliensis* subsp. *macrocalyx*), *19447* (*brasiliensis* subsp. *macrocalyx*), *19937* (*pauciflora*), *20304* (*pauciflora*), *20997* (*brasiliensis* subsp. *macrocalyx*), *22278* (*pauciflora*), *22383* (*pilosa*), *22771* (*pauciflora*), *25613* (*pilosa*), *26532* (*brasiliensis* subsp. *macrocalyx*), *28320* (*pilosa*), *32637* (*pauciflora*), *32869* (*pilosa*), *34918* (*pauciflora*), *37876* (*pilosa*), *39164* (*pilosa*), *39209* (*brasiliensis* subsp. *macrocalyx*), *40004* (*pauciflora*), *40470* (*pilosa*), *42939* (*brasiliensis* subsp. *brasiliensis*), *43192* (*australis*), *43273* (*pauciflora*), *43398* (*brasiliensis* subsp. *brasiliensis*), *43843* (*obovata* var. *coriacea*), *45295* (*pauciflora*), *45415* (*pilosa*), *515* (*pauciflora*)
Hatschbach & Ahumada 31333 (*brasiliensis* subsp. *brasiliensis*)
Hatschbach & Cervi 46844 (*pauciflora*)
Hatschbach & Guimarães 15286 (*pilosa*), *25473* (*pilosa*), *30302* (*cuneifolia*), *45004* (*brasiliensis* subsp. *brasiliensis*)
Hatschbach & Kummrow 37257 (*obovata* var. *obovata*), *45569* (*brasiliensis* subsp. *brasiliensis*)
Hatschbach & Pelanda 27941 (*uniflora*), *27993* (*brasiliensis* subsp. *brasiliensis*)
Hatschbach & Zelma 50296 (*rupestris*)
Heiner 209 (*pauciflora*), *s.n.* (*uniflora*)
Heinrichs 496 (*grandiflora* subsp. *schultesii*)
Henz 27246 (*pilosa*), *35305* (*pilosa*)
Heringer 10556 (*obovata* var. *coriacea*), 10719 (*obovata* var. *coriacea*), 11549 (*uniflora*), *460* (*hydrangeiformis* subsp. *capitata*), *8662* (*obovata* var. *coriacea*), *8993/1197* (*obovata* var. *coriacea*), *9096/1290* (*obovata* var. *coriacea*)
Heringer et al. 4281 (*obovata* var. *coriacea*), *6148* (*brasiliensis* subsp. *brasiliensis*)
Hermann 11237 (*grandiflora* subsp. *schultesii*)
Heyligers 438 (*guianensis*)
Hoehne, F. C. 582 (*pauciflora*), *23169* (*pauciflora*), *23309* (*pilosa*), *24405* (*pauciflora*), *4595* (*brasiliensis* subsp. *macrocalyx*), *4920* (*brasiliensis* subsp. *brasiliensis*), *5481* (*brasiliensis* subsp. *brasiliensis*), *6129* (*brasiliensis* subsp. *brasiliensis*), *6846* (*brasiliensis* subsp. *brasiliensis*), *7953* (*pauciflora*), *8250* (*brasiliensis* subsp. *macrocalyx*)
Hoehne, W., 6154 (*brasiliensis* subsp. *brasiliensis*), *6155* (*brasiliensis* subsp. *brasiliensis*)
Huber 14990 (*grandiflora* subsp. *grandiflora*), *1556* (*grandiflora* subsp. *grandiflora*), 1562 (*grandiflora* subsp. *grandiflora*), 4204 (*grandiflora* subsp. *schultesii*), *4377* (*grandiflora* subsp. *schultesii*), 4575 (*grandiflora* subsp. *grandiflora*), 4589 (*grandiflora* subsp. *grandiflora*), *887* (*guianensis*)
I.N.T.A. 4435 (*pilosa*)
Irwin 2269 (*brasiliensis* subsp. *brasiliensis*), *2674* (*uniflora*), *2701* (*uniflora*), *48753* (*grandiflora* subsp. *schultesii*)
Irwin et al. 13126 (*obovata* var. *coriacea*), *13194* (*brasiliensis* subsp. *brasiliensis*), *15799* (*brasiliensis* subsp. *brasiliensis*), *19549* (*brasiliensis* subsp. *brasiliensis*), *20150* (*brasiliensis* subsp. *brasiliensis*), *22077* (*rupestris*), *22465* (*rupestris*), *26556* (*brasiliensis* subsp. *brasiliensis*), *29189* (*brasiliensis* subsp. *brasiliensis*), *29407* (*brasiliensis* subsp. *brasiliensis*), *30628* (*brasiliensis* subsp. *brasiliensis*), *32406* (*uniflora*), *47359* (*grandiflora* subsp. *schultesii*), *47900* (*guianensis*), *55978* (*guianensis*), *8152* (*obovata* var. *coriacea*), *8514* (*obovata* var. *coriacea*)
Isabelle 6 (*pilosa*)
Jarenkow 132 (*cuneifolia*)
Johnston 71 (*uniflora*)
Johnston & Miller 265 (*uniflora*)
Joly 1133 (*brasiliensis* subsp. *brasiliensis*)
Jönsson, G. 1054a (*pilosa*)
Jorgensen 2098 (*australis*), *3661* (*australis*), *4 Oct. 1909* (*pilosa*), *Nov. 1910* (*pilosa*)
Juajibioy Chindoy 277 (*grandiflora* subsp. *schultesii*)
Jurgen 19 (*pilosa*)
Kennedy 1386 (*chiricaspi*), *316* (*dwyeri*)
Kermann 270 (*hydrangeiformis* subsp. *capitata*)
Kermes 1363 (*australis*)
Killip & Smith 26844 (*grandiflora* subsp. *schultesii*), *27667* (*grandiflora* subsp. *schultesii*), *28644* (*grandiflora* subsp. *schultesii*)
Klein 1751 (*pauciflora*), *319* (*pauciflora*), *3518* (*pilosa*), *4102* (*pilosa*), *4343* (*cuneifolia*)
Klein & Bresolin 6864 (*pauciflora*)
Klug 741 (*grandiflora* subsp. *schultesii*), *2880* (*grandiflora* subsp. *schultesii*), *3326* (*grandiflora* subsp. *schultesii*)
Krapovickas 29261 (*australis*)
Krapovickas & Cristobal 11706 (*australis*), *15385* (*australis*)

Krapovickas & Schinini 31476 (*boliviana*), *35155* (*grandiflora* subsp. *schultesii*)
Krapovickas et al. 26092 (*australis*)
Krukoff 1532 (*mire*), *5284* (*grandiflora* subsp. *grandiflora*)
Kuhlmann, J.G., 1326 (*mire*), 1327-k (*mire*), *141* (*obovata* var. *obovata*), 1722 (*guianensis*), 2287 (*mire*), *809* (*mire*), *943* (*amazonica*), *8 Nov. 1922* (*latifolia*), *19 Nov. 1928* (*uniflora*), *3 Feb. 1930* (*brasiliensis* subsp. *brasiliensis*), *24 Oct. 1932* (*hydrangeiformis* subsp. *hydrangeiformis*), *2 Apr. 1935* (*uniflora*), *10 Nov. 1943* (*uniflora*), *8 Oct. 1946* (*pilosa*)
Kuhlmann, M., 2176 (*pauciflora*), *2714* (*pauciflora*), *2926* (*obovata* var. *obovata*), *4309* (*brasiliensis* subsp. *macrocalyx*), *4359* (*brasiliensis* subsp. *macrocalyx*)
Kummrow 1575 (*pauciflora*), *2420* (*pauciflora*), *2432* (*cuneifolia*), *94* (*pilosa*), *970* (*brasiliensis* subsp. *macrocalyx*)
Lalandes s.n. (*brasiliensis* subsp. *brasiliensis*)
Landrum et al. 4150 (*brasiliensis* subsp. *brasiliensis*)
Langsdorff 43 (*hydrangeiformis* subsp. *hydrangeiformis*), s.n. (*brasiliensis* subsp. *brasiliensis*), s.n. (*hydrangeiformis* subsp. *hydrangeiformis*)
Lanjouw 345 (*guianensis*)
Lanjouw & Lindeman 2137 (*guianensis*), *2564* (*guianensis*), *2888* (*guianensis*)
Leite 3660 (*pauciflora*), *4188* (*hydrangeiformis* subsp. *hydrangeiformis*)
Lemme s.n. (*guianensis*)
Levy 12 (*pauciflora*)
Lima, A. S. 7859 (*mire*)
Lima, D. de A., 52-1039 (*uniflora*)
Lima, H. C. de, and Ramamoorthy 1224 (*brasiliensis* subsp. *brasiliensis*)
Lima, H. C. de, et al. 1637 (*uniflora*)
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Lindberg 203 (*uniflora*)
Lindeman 5889 (*guianensis*), *6069* (*guianensis*), *6162* (*guianensis*)
Lindeman & Haas 1174 (*brasiliensis* subsp. *macrocalyx*), *3248* (*pilosa*), *5157* (*brasiliensis* subsp. *macrocalyx*)
Lindeman et al. 8233 (*pilosa*)
Lindeman, C. A-597-a (*australis*), *A-597-b* (*pilosa*), *A-597-c* (*pilosa*)
Llamas 1530 (*pilosa*)
Llamas sp. nov. (*australis*)
Lobb 65 (*grandiflora* subsp. *grandiflora*), *s.n.* (*brasiliensis* subsp. *brasiliensis*), *s.n.* (*hydrangeiformis* subsp. *capitata*)
Löfgren 86 (*brasiliensis* subsp. *brasiliensis*), *389* (*pilosa*), *3986* (*brasiliensis* subsp. *brasiliensis*), *948* (*pauciflora*)
Löfgren & Cowan 1660 (*pauciflora*)
Löfgren & Edwall 1435 (*uniflora*), *2705* (*pauciflora*)
Longfield 367 (*macrocarpa*)
Lorentz & Hieronymus 258 (*uniflora*)
Luderwaldt 1086 (*brasiliensis* subsp. *brasiliensis*), *2117* (*pilosa*)
Lugo 23 (*grandiflora* subsp. *grandiflora*), *2724* (*chiricaspi*), *2942* (*chiricaspi*), *2981* (*chiricaspi*), *3476* (*chiricaspi*)
Lund 754 (*brasiliensis* subsp. *brasiliensis*), *755* (*obovata* var. *obovata*), *756* (*brasiliensis* subsp. *brasiliensis*)
Luschnath Sep. 1833 (*uniflora*), *Nov. 1833* (*uniflora*), *s.n. 1832* (*brasiliensis* subsp. *brasiliensis*), *s.n. 1834* (*brasiliensis* subsp. *brasiliensis*), *s.n. 1834* (*latifolia*)
Luteyn et al. 4769 (*grandiflora* subsp. *grandiflora*)
Lutz 1551 (*hydrangeiformis* subsp. *capitata*), *Jan. 1925* (*brasiliensis* subsp. *brasiliensis*), *Boc 14* (*hydrangeiformis* subsp. *capitata*)
Lützelburg 4019 (*obovata* var. *coriacea*), *6187* (*brasiliensis* subsp. *macrocalyx*) *6495* (*hydrangeiformis* subsp. *capitata*), *6559* (*brasiliensis* subsp. *macrocalyx*)
Maas et al. 12963 (*grandiflora* subsp. *grandiflora*), *3326* (*hydrangeiformis* subsp. *hydrangeiformis*), *P12709* (*grandiflora* subsp. *grandiflora*), *P13228* (*grandiflora* subsp. *schultesii*)
Macedo 3131 (*brasiliensis* subsp. *brasiliensis*), *5 Feb. 1948* (*uniflora*)
Madison 986 (*mire*)
Madison et al. 5390 (*grandiflora* subsp. *schultesii*)
Magalhães 1643 (*hydrangeiformis* subsp. *hydrangeiformis*)
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Markgraf 3495 (*brasiliensis* subsp. *brasiliensis*)
Markgraf & Apparicio 10495 (*hydrangeiformis* subsp. *capitata*)
Martinelli 1115 (*hydrangeiformis* subsp. *hydrangeiformis*), *5135* (*uniflora*)
Martinelli et al. 5665 (*uniflora*)
Martius 1292 (*brasiliensis* subsp. *brasiliensis*), *3300* (*martiana*), *541* (*bonodora*), *Dec. 1817* (*brasiliensis* subsp. *brasiliensis*), *s.n.* (*guianensis*), *s.n.* (*martiana*), *s.n.* (*uniflora*)
Matthews 1320 (*grandiflora* subsp. *schultesii*)

Mattos Silva et al. 357 (*clandestina*)
Mattos, J., & Mattos, N., 14284 (*brasiliensis* subsp. *brasiliensis*)
McDaniel 15328 (*grandiflora* subsp. *schultesii*)
Melin 186 (*grandiflora* subsp. *schultesii*)
Mello Barreto 10530 (*brasiliensis* subsp. *brasiliensis*), *7767* (*brasiliensis* subsp. *brasiliensis*), *7784* (*brasiliensis* subsp. *brasiliensis*), *7786* (*brasiliensis* subsp. *brasiliensis*), *7788* (*brasiliensis* subsp. *brasiliensis*), *7789* (*brasiliensis* subsp. *brasiliensis*), *7791* (*brasiliensis* subsp. *brasiliensis*), *7793* (*brasiliensis* subsp. *brasiliensis*), *7794* (*brasiliensis* subsp. *brasiliensis*), *9063* (*brasiliensis* subsp. *brasiliensis*), *9479* (*rupestris*), *9833* (*brasiliensis* subsp. *brasiliensis*)
Mello Filho 793 (*pilosa*)
Mexia 4089-a (*hydrangeiformis* subsp. *capitata*), *4551* (*uniflora*), *5182* (*uniflora*), *5467* (*brasiliensis* subsp. *brasiliensis*), *6444* (*grandiflora* subsp. *schultesii*), *7275* (*grandiflora* subsp. *grandiflora*)
Meyer 12621 (*australis*), *166* (*australis*), *3076* (*australis*)
Miers 4495 (*brasiliensis* subsp. *brasiliensis*), *4721* (*uniflora*), *Dec. 1837* (*hydrangeiformis* subsp. *capitata*), *Feb. 1838* (*brasiliensis* subsp. *macrocalyx*), *s.n. 1838* (*hydrangeiformis* subsp. *capitata*)
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Mimura 53 (*brasiliensis* subsp. *brasiliensis*)
Montes 27471 (*australis*), *4703* (*australis*)
Mora 1040 (*chiricaspi*)
Moreira 5775 (*brasiliensis* subsp. *brasiliensis*), *s.n.* (*brasiliensis* subsp. *macrocalyx*)
Morel 3783 (*australis*), *4144* (*australis*), *8921* (*australis*)
Mori 6828 (*chocoensis*)
Mori & Bolten 8394 (*guianensis*), *8575* (*guianensis*)
Mori & Boom 14726 (*guianensis*), *14834* (*guianensis*)
Mori et al. 12082 (*clandestina*), *8767* (*guianensis*), *9775* (*clandestina*)
Moura s.n., 1887 (*hydrangeiformis* subsp. *hydrangeiformis*)
Mosen 673 (*uniflora*)
Mueller 435 (*pauciflora*)
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Neill 6546 (*grandiflora* subsp. *grandiflora*)
Neill & Palacios 7101 (*grandiflora* subsp. *grandiflora*)
Netto s.n. (*brasiliensis* subsp. *brasiliensis*)
Netto et al. s.n. (*brasiliensis* subsp. *brasiliensis*)
Neuwied, Pr. von s.n. 1827 (*uniflora*)
Noblick 2038 (*uniflora*)
Occhioni 1131 (*brasiliensis* subsp. *macrocalyx*), *9174* (*brasiliensis* subsp. *brasiliensis*)
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Oliveira 21 (*brasiliensis* subsp. *brasiliensis*)
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Pabst 5393 (*pauciflora*), *7411* (*brasiliensis* subsp. *brasiliensis*), *8340* (*brasiliensis* subsp. *brasiliensis*), *9115* (*brasiliensis* subsp. *brasiliensis*)
Pabst & Brade 10283 (*brasiliensis* subsp. *macrocalyx*)
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Paiva & Stehmann s.n. (*australis*)
Palacios et al. 3467 (*brasiliensis* subsp. *brasiliensis*)
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Peckolt, O., Aug. 1934 (*hydrangeiformis* subsp. *hydrangeiformis*)
Peckolt, T., 71 (*hydrangeiformis* subsp. *capitata*)
Pedersen 418 (*australis*), *418a* (*australis*)
Pereira 6066 (*pauciflora*), *9241* (*hydrangeiformis* subsp. *hydrangeiformis*), *9451* (*brasiliensis* subsp. *brasiliensis*)
Pérez Arbelaez 688 (*grandiflora* subsp. *schultesii*)
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Pickel 2200 (*uniflora*), *670* (*uniflora*)
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Pinheiro 1980 (*clandestina*), *2086* (*clandestina*)
Pinkley 202 (*grandiflora* subsp. *grandiflora*), *420* (*chiricaspi*), *43* (*grandiflora* subsp. *grandiflora*), *444* (*grandiflora* subsp. *schultesii*), *457* (*grandiflora* subsp. *schultesii*), *460* (*grandiflora* subsp. *grandiflora*), *563* (*chiricaspi*), *575* (*grandiflora* subsp. *schultesii*)
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Plaumann 164 (*pilosa*)
Plowmann 10020 (*obovata* var. *coriacea*), *1911* (*uniflora*), *1919* (*imatacana*), *2039* (*grandiflora* subsp. *schultesii*), *2080* (*chiricaspi*), *2081* (*chiricaspi*), *2090* (*grandiflora* subsp. *schultesii*), *2092* (*chiricaspi*), *2183* (*grandiflora* subsp. *schultesii*), *2494* (*grandiflora* subsp. *schultesii*), *2713* (*australis*), *2723* (*australis*), *2735* (*pilosa*), *2739* (*pauciflora*), *3160* (*dwyeri*), *5825* (*grandiflora* subsp. *schultesii*), *5984* (*grandiflora* subsp. *schultesii*)

Plowman & Davis 4852 (*mire*), *5000* (*mire*), *5036* (*mire*), *5172* (*mire*)
Plowman & de Lima, H.C., 12901 (*hydrangeiformis* subsp. *capitata*)
Plowman & Kennedy 2310 (*grandiflora* subsp. *schultesii*)
Plowman & Sucre 2786 (*brasiliensis* subsp. *brasiliensis*), *2891* (*brasiliensis* subsp. *macrocalyx*), *2906* (*brasiliensis* subsp. *macrocalyx*)
Plowman et al. 10066 (*clandestina*), 10087 (*clandestina*), *2404* (*grandiflora* subsp. *schultesii*), *2407* (*grandiflora* subsp. *schultesii*), *6455* (*grandiflora* subsp. *schultesii*), *6737* (*grandiflora* subsp. *schultesii*), *6939* (*grandiflora* subsp. *schultesii*)
Poeppig 2206 (*grandiflora* subsp. *schultesii*)
Pohl 263 (*brasiliensis* subsp. *brasiliensis*), *264* (*uniflora*), *265* (*brasiliensis* subsp. *brasiliensis*), *266* (*brasiliensis* subsp. *brasiliensis*), *s.n.* (*uniflora*)
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Prance & Silva 59030 (*obovata* var. *coriacea*)
Prance et al. 11611 (*martiana*), 11998 (*grandiflora* subsp. *grandiflora*), 13471 (*grandiflora* subsp. *grandiflora*), 14551 (*grandiflora* subsp. *schultesii*), *3880* (*amazonica*), *4704* (*martiana*), *5854* (*grandiflora* subsp. *schultesii*), *6570* (*grandiflora* subsp. *schultesii*), *6933* (*cuneifolia*), *8265* (*mire*), *9553* (*uniflora*)
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Raben 14 (*hydrangeiformis* subsp. *hydrangeiformis*), *703* (*brasiliensis* subsp. *brasiliensis*), *746* (*pauciflora*)
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Rambo 29147 (*australis*), *321* (*australis*), *37819* (*australis*), *44295* (*pilosa*), *49144* (*pilosa*)
Regnell 173 (*brasiliensis* subsp. *brasiliensis*), *I-374* (*uniflora*), *I-375* (*brasiliensis* subsp. *brasiliensis*)
Reiss 99 (*pilosa*)
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Reitz & Klein 11250 (*australis*), *1158* (*pauciflora*), *14136* (*pilosa*), *16178* (*cuneifolia*), *2160* (*pauciflora*), *4076* (*cuneifolia*), *4238* (*pauciflora*), *5601* (*pauciflora*), *7329* (*pauciflora*), *7601* (*brasiliensis* subsp. *macrocalyx*), *9205* (*pauciflora*)
Revilla 1724 (*grandiflora* subsp. *schultesii*), *304* (*grandiflora* subsp. *schultesii*)
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Santos, N. 5790 (*latifolia*)
Santos, T. Soares dos, 2511 (*uniflora*), *1964* (*clandestina*), *2015* (*clandestina*), *433* (*clandestina*), *689* (*clandestina*)
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Santos Lima Aug. 1940 (*pauciflora*)
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Uribe, P., Dec. 1930 (*grandiflora* subsp. *schultesii*)
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Wawra & Maly 426 (*brasiliensis* subsp. *brasiliensis*)
Weberbauer 6151 (*grandiflora* subsp. *grandiflora*)
Weddell 1648 (*brasiliensis* subsp. *brasiliensis*), *3621* (*boliviana*), *818* (*hydrangeiformis* subsp. *capitata*), *878* (*hydrangeiformis* subsp. *hydrangeiformis*), *s.n. 1844* (*uniflora*), *s.n. 1858* (*uniflora*)
Weir 23 (*brasiliensis* subsp. *brasiliensis*)
Wessels Boer 1195 (*guianensis*)
Wettstein & Schiffner Sep. 1901 (*pauciflora*), *s.n.* (*brasiliensis* subsp. *brasiliensis*)
White 1072 (*mire*), *1840* (*grandiflora* subsp. *schultesii*), *2386* (*grandiflora* subsp. *schultesii*)
Widgren 486 (*brasiliensis* subsp. *brasiliensis*), *596* (*hydrangeiformis* subsp. *capitata*), *s.n. 1844* (*hydrangeiformis* subsp. *capitata*), *s.n. 1845* (*uniflora*)
Wilbur & Weaver 11358 (*dwyeri*)
Williams & Assis 6088 (*brasiliensis* subsp. *brasiliensis*), *6859* (*brasiliensis* subsp. *brasiliensis*), *7928* (*hydrangeiformis* subsp. *hydrangeiformis*), *12 Feb. 45* (*brasiliensis* subsp. *brasiliensis*)
Williams, L. 5482 (*grandiflora* subsp. *schultesii*)
Woolston 571 (*australis*)
Woytkowksi 34536 (*grandiflora* subsp. *grandiflora*), *35008* (*grandiflora* subsp. *schultesii*), *5026* (*grandiflora* subsp. *grandiflora*), *514* (*grandiflora* subsp. *grandiflora*) *5525* (*grandiflora* subsp. *schultesii*), *6170* (*grandiflora* subsp. *schultesii*)
Wüllschlagel 1505 (*guianensis*)
Ybarrola 2963 (*australis*), *3270* (*australis*), *3430* (*australis*)
Zarucchi & Andrade 2316 (*grandiflora* subsp. *grandiflora*)
Zaruma et al. 56 (*chiricaspi*)
Zernys s.n. (*brasiliensis* subsp. *macrocalyx*)

Appendix II: *Brunfelsia* sect. *Brunfelsia*

Description

Brunfelsia L. sect. *Brunfelsia*. Type species: *B. americana* L.

Brunfelsia L., Sp. Pl. 191. 1753. Type species: *B. americana* L.

Brunfelsia L. sect. *Eubrunfelsia* Griseb, Fl. Brit. W. Ind. 432. 1861. Type species: *B. americana* L.

Brunfelsia L. subg. *Brunfelsiopsis* Urb., Symb. Ant. 1: 402. 1899. Type species: *B. densifolia* Krug & Urb.

Brunfelsiopsis (Urb.) Kuntze in Post & Kuntze, Lex. 81. Dec. 1903 ("1904"). Type species: *B. densifolia* Krug & Urb.

Brunfelsia sect. *Brunfelsiopsis* (Urb.) Dalla Torre & Harms, Gen. Siphon. 453. 1904. Type species: *B. densifolia* Krug & Urb.

Shrubs or small trees to 10 m tall. **Inflorescence** terminal or axillary. **Flowers** large, 1–many per inflorescence. **Corolla** white, turning yellow with age, or reddish purple; tube 6–24 times as long as calyx, gradually dilated toward apex, open, not constricted at mouth. **Anthers** oblong, weakly bilobate. **Stigma** subcapitate, convex, subentire or shallowly bilobate. West Indies (see Fig. 9). About 20 species.[17]

Names of Brunfelsia Sect. Brunfelsia

Brunfelsia acunae Hadac, Fol. Geobot. Phytotax. 5: 430. 1970.

Brunfelsia americana L., Sp. Pl. 191. 1753. (*B. terminalis* Salisb., Prodr. Stirp. 109. 1796. *B. violacea* Lodd, Bot. Cab., t. 792. 1823. *B. inodora* Mart., Del. Sem. Hort. Monac. 1847; Linnaea 24: 180. 1851. *B. fallax* Duchass. ex Griseb., Abh. Konigl. Ges. Wiss. Gottingen. 7: 242. 1857. *B. americana* var. *pubescens* Griseb., Fl. Brit. W. Ind. 432. 1864. *B. abbottii* Leonard, J. Wash. Acad. Sci. 17(3): 71. 1927.) Lesser Antilles, Puerto Rico, Dominican Republic.

Brunfelsia cestroides A. Rich., Fl. Cub. Fan. 3: 151. 1853. (*B. vinciflora* Griseb., Mem. Am. Acad. Arts 8(1): 523. 1860.) Cuba.

Brunfelsia clarensis Britton & P. Wilson, Mem. Torrey Bot. Club 16(2): 102. 1920. Cuba.

Brunfelsia densifolia Krug & Urb., Notizbl. Konigl. Bot. Gart. Berlin 1(10): 324. 1897. Puerto Rico.

Brunfelsia grisebachii Amshoff, Contrib. Ocas.

[17] This Caribbean group of brunfelsias is being revised at present by Victor Fuentes Fiallo of INIFAT, Havana, Cuba.—*Eds.*

Mus. Hist. Nat. Col. "De la salle," Habana 15: 6. 1956. Cuba.

Brunfelsia jamaicensis (Benth.) Griseb., Fl. Brit. W. Ind. 432. 1864. (*B. nitida* var. *jamaicensis* Benth. in DC., Prodr. 10: 201. 1846. *B. harrisii* Urb., Symb. Ant. 3: 373. 1903.) Jamaica.

Brunfelsia lactea Krug & Urb., Notizbl. Bot. Gart. Berlin 1(10): 323. 1897. Puerto Rico.

Brunfelsia linearis Ekman, Feddes Repert. Spec. Nov. Regni Veg. 21: 223. 1925. Cuba.

Brunfelsia macroloba Urb., Symb. Ant. 9: 252. 1924. Cuba.

Brunfelsia maliformis Urb., Symb. Ant. 3: 372. 1903. (*B. fawcettii* Urb, Symb. Ant. 3: 371. 1903.) Jamaica.

Brunfelsia membranacea Urb., Symb. Ant. 5: 491. 1908. Jamaica.

Brunfelsia nitida Benth. in DC., Prodr. 10: 201. 1846. (*B. parvifolia* A. Rich., Fl. Cub. Fan. 3: 151. 1853. *B. longituba* Lem., Jard. Fleur. 4: 61. 1854.) Cuba.

Brunfelsia picardae Krug & Urb., Notizbl. Bot. Gart. Berlin 1(10): 321. 1897. Haiti.

Brunfelsia plicata Urb., Symb. Ant. 6: 39. 1909. Jamaica.

Brunfelsia pluriflora Urb., Symb. Ant. 9: 252. 1924. Cuba.

Brunfelsia portoricensis Krug & Urb., Notizbl. Bot. Gart. Berlin 1(10): 322. 1897. Puerto Rico.

Brunfelsia purpurea Griseb., Mem. Ann. Acad. Arts n. s. 8(1): 523. 1869. Cuba.

Brunfelsia shaferi Britton & P. Wilson, Mem. Torrey Bot. Club 16(2): 102. 1920. Cuba.

Brunfelsia sinuata A. Rich., Fl. Cub. Fan. 3: 151, t. 66. 1853. Cuba.

Brunfelsia splendida Urb., Symb. Ant. 5: 491. 1908. Jamaica.

Brunfelsia undulata Sw., Nov. Gen. Spec. Pl. 90. 1788. Jamaica.

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Synonyms and non-English common names are *italicized.* New names or combinations are in **boldface.** Page numbers for illustrations are also in **boldface.**

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